



VULNERABILITY OF YEARLING AND 2-YEAR-OLD BULL MOOSE TO TWO ANTLER BASED HARVEST REGULATIONS IN BRITISH COLUMBIA

Daniel A. Aitken¹, Ian W. Hatter², Roy V. Rea³, and Kenneth N. Child⁴

¹College of New Caledonia, 3330 22nd Avenue, Prince George, British Columbia V2N 1P8; ²49-640 Upper Lakeview Road, Invermere, BC V0A 1K3, Canada; ³Natural Resources and Environmental Studies Institute, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia V2N 4Z9, Canada; ⁴6372 Cornell Place, Prince George, British Columbia V2N 2N7 Canada.

ABSTRACT: A spike-fork (S/F) general open season (GOS) for bull moose (*Alces alces*) was introduced with a lottery draw, limited entry hunting (LEH) in the Omineca (1981), Thompson (1993), and Okanagan (1993) regions of British Columbia. The S/F regulation permitted harvest of a bull having no more than two tines on one antler, including the tines on the main antler and brow palms; the LEH controlled the harvest of bulls with antlers $>$ S/F. In the Peace region, the S/F regulation was implemented (1996) as part of SOFT regulations which permitted harvest of bulls with spike, fork, or antlers with 3 or more points on either brow palm; in 2003, SOFT10 regulations permitted the harvest of bull moose with ≥ 10 points on one or both antlers. These combinations with the S/F regulation were meant to control annual harvest of bulls, maintain herd social structure, and maximize recreational opportunity. We used age and antler point data collected through a Voluntary Tooth Return Program (VTRP) from 1988 to 2003 ($n = 39,325$) to assess vulnerability of yearlings ($n = 12,743$) and 2-year-olds ($n = 8,712$) to the S/F regulation as well as a hypothetical spike-only regulation. For each age class, we defined potential vulnerability to the S/F regulation as the proportion of bulls in the harvest with S/F antlers when no antler-based restrictions were in place. We similarly defined potential vulnerability to the spike-only regulation as the proportion of bulls in the harvest with at least one spike antler. Potential vulnerability across British Columbia to the spike-fork regulation was 43% for yearlings and 10% for 2-year-old bulls, whereas potential vulnerability to the spike-only regulation was 8% for yearlings and 1% for 2-year-old bulls. Realized vulnerability to harvest of each age class was defined as the proportion of that age class with spike-fork antlers when there were spike-fork regulations combined with either LEH or other antler-based restrictions. Similarly, realized vulnerability to harvest for spike-only bulls in each age class was the proportion of harvested bulls with at least one spike antler when spike-fork regulations were combined with either LEH or as part of the SOFT or SOFT10 regulations. Realized vulnerability across British Columbia to the S/F regulation was 49% for yearlings and 7% for 2-year-old bulls; realized vulnerability to the spike-only regulation was 9% for yearlings and 1% for 2-year-old bulls. Potential vulnerabilities and realized vulnerabilities varied regionally and annually, which may reflect different subspecies of moose (*A. a. shirasi*, *A. a. andersoni*, *A. a. gigas*) with different antler architectures, but more likely, differences related to habitat quality across the latitudinal breadth of British Columbia. The S/F regulation provides hunting opportunity, but combined with other hunting seasons/regulations, may not provide adequate protection of yearling and 2-year-old bulls in some regions. The spike-only regulation exposes fewer yearling and 2-year-old bulls to harvest and offers an alternative to regulate bull harvests while maintaining hunter opportunity.

ALCES VOL. 57: 139–166 (2021)

Key words: *Alces alces*, antler regulations, bull moose, hunting, spike-fork, spike-only, vulnerability, yearling bull

Licensed hunting of moose (*Alces alces*) in North America has traditionally focused on harvesting bull moose (bulls) with temporal restrictions on harvest of antlerless animals in a population (Timmermann 1987). A departure from this tradition was implemented in the Omineca region of central British Columbia (Macgregor and Child 1981) when regulations were modified to institute selective harvest of *A. a. andersoni*. These regulations were designed to address differential harvest of sexes and age classes focusing on calves, cows, and immature and mature bulls (Bubenik 1971, Child 1983, Child and Aitken 1989). Beginning in 1981, the general open season (GOS) afforded hunters the opportunity to harvest either a calf or spike-fork (S/F) bull, with other bulls and cows harvested through a lottery draw or limited entry hunt (LEH). The S/F regulation permitted harvest of bulls having no more than 2 tines on one antler, including tines on the main antlers and brow palms (BC Ministry of Environment 1981–1982); essentially, this approach directed hunters to focus harvesting on smaller antlered yearlings and 2-year-old bulls (Child et al. 2010a, 2010b).

In combination, these regulations were intended to control harvest of bulls, maximize recreational opportunity, and maintain a balanced social structure (i.e., maintain prime bulls) to improve herd productivity (Child 1983, Bubenik 1985, 1987, Aitken and Child 1992, Boer 1992, Timmermann 1992, Child 1996). While focussed harvest on young/immature bulls combined with controlled harvest of older/mature bulls is a desired outcome of selective harvesting, it is also important to ensure that yearlings and 2-year-old bulls are in sufficient supply to be recruited into older age classes to maintain desired breeding sex ratios and age structure. Previous assessments of the S/F regulation in the Omineca region indicated that this

antler-based regulation, in combination with a controlled harvest of older/mature bulls, held promise as an effective harvest strategy to control harvest of bulls while providing moderate levels of hunting recreation (Hatter and Child 1992, Hatter 1998, 1999, Demarchi and Hartwig 2008). The S/F regulation had been used in Alaska since 1987 as part of a Selective Harvest System (SHS) (Schwartz et al. 1992) to regulate harvests of *A. a. gigas*, but was suspended in 2011 and 2012 over concern of skewed bull:cow ratios. It was replaced with a spike-only regulation in several areas in 2013 (Robertia 2013) remaining in use to the present day (Alaska Department of Fish and Game 2020–2021).

The predominant sub-species of moose throughout British Columbia is *Alces alces andersoni* with *A. a. shirasi* found in the extreme southeastern corner of the province (Eastman and Ritcey 1987). Although *A. a. gigas* was thought to occur at the extreme northwestern corner of British Columbia (Eastman and Ritcey 1987), recent genetic analyses (Hundtermark et al. 2006, Colson 2013, DeCesare et al. 2020) suggests that *A. a. andersoni* extends further northwest than previously believed. Gasaway et al. (1987) reported that mean antler size of prime bulls was smallest in *A. a. shirasi*, intermediate in *A. a. andersoni*, and largest in *A. a. gigas*. However, DeCesare et al. (2020) suggested that environmental factors rather than genetic differences were the primary influence of observed differences in antler size between these subspecies. Since antlers vary with age and body size (Gasaway et al. 1987, Stewart et al. 2000, Bowyer et al. 2002, Child et al. 2010a, Jensen et al. 2013, Andreozzi et al. 2015), and presumably between subspecies (Gasaway et al. 1987), we expect that the prevalence of S/F antlers would be highest in *A. a. shirasi*, intermediate in *A. a. andersoni*, and lowest in *A. a. gigas*. Furthermore, we expect more S/F antlers in yearlings

compared to 2-year-olds, as well as in moose from southern versus northern areas across the distribution of *A. a. andersoni*.

The purpose of this study was to examine vulnerability to the S/F regulation from 1988 to 2003 of both yearling and 2-year-old bull moose within 7 specific wildlife management regions and across the province of British Columbia. We examined whether the S/F regulation was equally effective in all years and regions given the presence of different subspecies of moose, as well as the extensive geographical ranges and the 15-year period of study. The vulnerabilities of the subspecies found within British Columbia were examined by comparing the vulnerabilities of *A. a. shirasi* in the eastern portions of the Kootenay region to those of *A. a. andersoni* in the western portions of the Kootenay region, and by comparing the vulnerabilities of *A. a. gigas* in the north-western portion of the Skeena region with those of *A. a. andersoni* in adjacent areas of that region. Differences in vulnerabilities were compared in the range of *A. a. andersoni* from south (49th parallel) to north (60th parallel) across British Columbia. We also evaluated temporal trends in vulnerabilities of yearlings and 2-year-old bulls to the S/F regulation within British Columbia, and make recommendations about its continued use. We also examined the vulnerability of yearlings and 2-year-old bulls to a hypothetical spike-only regulation (a bull having no more than 1 tine on one antler) to evaluate that as an alternative to the S/F regulation if overharvest of yearling or 2-year-old bull moose occurred under the S/F regulation.

STUDY AREA

We assessed vulnerability of yearling and 2-year-old bull moose to antler-based regulations from 1988 to 2003 in 7 Wildlife administrative regions of British Columbia:

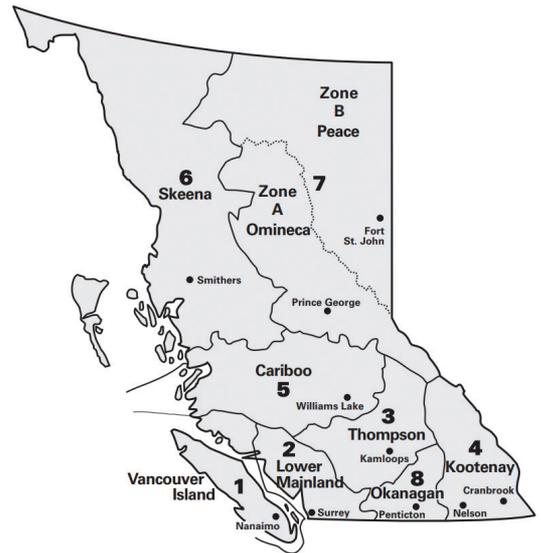


Fig. 1. Wildlife administrative regions of British Columbia, Ministry of Forests, Lands, Natural Resource Operations and Rural Development (from the BC Hunting and Trapping Regulations Synopsis 2018–2020). The study area included 7 regions: 3 Thompson, 4 Kootenay, 5 Cariboo, 6 Skeena, 7 Zone A Omineca, 7 Zone B Peace, and 8 Okanagan.

Kootenay, Okanagan, Thompson, Cariboo, Omineca¹, Skeena, and Peace¹ (Fig. 1). These regions exhibit a wide variety of landforms from high mountain peaks interspersed with rolling plateaus to alluvial valleys (Church and Ryder 2010). The majority of our study area lies within the Montane Cordillera and Boreal Cordillera Ecozones, with the Taiga Plains and Boreal Plains in the far northeast and the Semi-Arid Plateau to the southwest (Canadian Council on Ecological Areas 2014). The administrative regions vary physio-graphically, ecologically, and climatically with forest cover types and moose habitat use patterns varying by region (Eastman and Ritcey 1987).

¹Note: Although the Omineca and Peace are zones A and B within Region 7, we refer to them as the Omineca region and Peace region throughout the article.

Table 1. Temporal and regional summary of any bull general open season (GOS), any bull limited entry hunt (LEH), and spike-fork (S/F) general open season hunting regulations used in regions of British Columbia (1988 to 2003).

| Region | Any bull GOS or LEH | S/F GOS combined with LEH |
|--------------------|----------------------|---------------------------|
| Kootenay | 1988–2003 | not used |
| Okanagan | 1988–1992 | 1993–2003 |
| Thompson | 1988–1992 | 1993–2003 |
| Cariboo | 1988–2003 | not used |
| Omineca | not used | 1988–2003 |
| Skeena | 1988–2003 | not used |
| Peace ¹ | 1988–1995, 1996–2003 | 1996–2003 |

¹Any bull GOS August to October 1988–1995, any bull GOS August 1996–2003, SOFT bull September to October 1996–2002, SOFT10 bull September to October 2003.

Harvests of bulls throughout the study regions were regulated with a mix of GOS, LEH, and/or S/F seasons (Hatter 1998, 1999, Demarchi and Hartwig 2008; Table 1). The S/F antler point restriction was employed in the Omineca region throughout the study and was later adopted in the Thompson (1993), Okanagan (1993), and Peace (1996) regions. The Omineca, Thompson, and Okanagan regions combined the S/F GOS with a LEH that did not employ antler point restrictions. In contrast, starting in 1996, the Peace region combined a S/F GOS with a GOS that included antler point restrictions. Prior to 1996, an any-bull GOS was advertised in the Peace Region from 15 August to 31 October each year; from 1996 to 2003, the any-bull GOS was retained for the period of 15 to 31 August. The harvest in September and October from 1996 to 2002 was subject to the SOFT regulation which permitted the harvest of bulls with spike or fork antlers (SOF) or having at least one antler with a brow palm bearing ≥ 3 points (T) (BC Ministry of Environment 1996–1997; Fig. 2). In 2003, SOFT was modified to the SOFT10 regulation (Poole and DeMars 2015) which permitted harvest of bulls with at least one antler with a minimum of 10 points, in addition to those with spike or fork antlers (SOF), or with ≥ 3 points on either brow palm (T) (BC

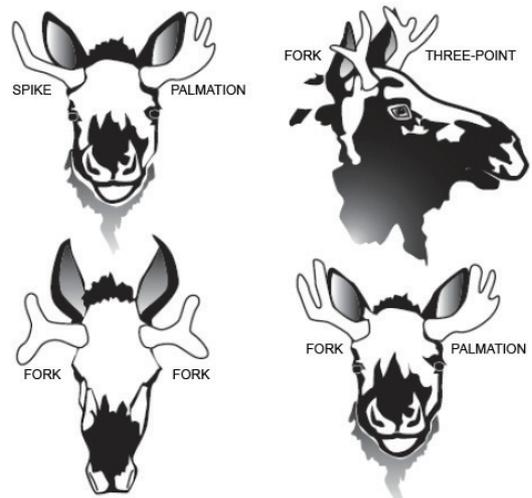


Fig. 2. Antler architectures with configurations labelled for yearling or 2-year-old bull moose in British Columbia (adapted from the Hunting and Trapping Regulations Synopsis in BC Ministry of Environment 2018–2020).

Ministry of Water, Land and Air Protection 2003–2004). The Cariboo and Skeena regions did not employ antler point restrictions with either GOS or LEH.

METHODS

Age and antler point data for assessing the effects of antler regulations on yearling and 2-year-old bulls were obtained from the Voluntary Tooth Return Program (VTRP)

that operated from 1988 to 2003, except for 1999 when it was temporarily suspended. A harvest data card envelope was provided to hunters upon purchase of their moose hunting licence or mailed with LEH authorization. Hunters could record specifics of their hunt including the management unit (MU), date and sex of kill, and the number of antler points on the left and right antlers. Instructions were provided for removing a lower incisor tooth that was sealed within the envelope and mailed (postage paid) to the provincial wildlife management agency. Hunters submitting a tooth received a “Management Participant” jacket crest. Age was determined from cementum annuli inspections (Sergeant and Pimlott 1959) performed by regional technicians and contractors.

We used the VTRP data to separately calculate the vulnerability of 2 age classes of bull moose (yearling or 2-year-old) to two regulations (S/F or spike-only) in two different ways (potential or realized vulnerability). Generally, vulnerability was calculated as the proportion of the harvest of each age class that consisted of bull moose with antlers of the specified configuration. Potential vulnerability to each regulation was calculated when all bulls were legal to hunt without antler restrictions, either under a GOS or a LEH (Table 1). Potential vulnerability of each age class to the S/F regulation was

defined as the proportion of bulls in the harvest with S/F antlers when no antler based restrictions to harvest were in place during a GOS or LEH. Similarly, potential vulnerability of each age class to the spike-only regulation was defined as the proportion of bulls in the harvest with spike-only antlers when no antler based restrictions to harvest were in place during a GOS or LEH (Table 2). Realized vulnerability to each regulation was calculated for the Okanagan, Thompson, Omineca, and Peace regions when the S/F regulation was in effect with other regulations allowing harvest of bull moose (Table 1). For the Okanagan, Thompson, and Omineca regions, realized vulnerability of each age class to the S/F regulation was defined as the proportion of the harvest with S/F antlers when S/F regulations were combined with LEH regulations. Similarly, realized vulnerability of each age class to the spike-only regulation was defined as the proportion of the harvest with spike-only antlers when S/F regulations were combined with LEH regulations (Table 2). Realized vulnerability to each regulation for the Peace region was similarly calculated when the S/F regulation was in effect as part of the SOFT or SOFT10 regulations (Table 1). When the SOFT regulations were in effect the total harvest of bulls of each age class consisted of bulls with S/F antlers and bulls with

Table 2. Equations used to calculate potential vulnerability and realized vulnerability to the S/F regulations and to the spike-only regulation for both yearling and 2-year-old bull moose in British Columbia.

| Regulation | Potential vulnerability Any bull GOS or LEH | Realized vulnerability | |
|------------|--|---|---|
| | | S/F GOS and any bull LEH | SOFT |
| S/F | $= \frac{SF \text{ in age class } X}{\text{all age class } X}$ | $= \frac{SF \text{ in age class } X}{SF \text{ in age class } X + \text{any bull in age class } X}$ | $= \frac{SF \text{ in age class } X}{SOFT \text{ bulls in age class } X}$ |
| Spike-only | $= \frac{Spike \text{ only in age class } X}{\text{all age class } X}$ | $= \frac{Spike \text{ only in age class } X}{SF \text{ in age class } X + \text{any bull in age class } X}$ | $= \frac{Spike \text{ only in age class } X}{SOFT \text{ bulls in age class } X}$ |

¹The SOFT regulation was used in the Peace region from 1996 to 2002 while the SOFT10 regulation was introduced in 2003. For 2003, the realized vulnerability for the Peace region was calculated by replacing the number of SOFT bulls in the denominator with the number of SOFT10 bulls.

tri-palm antlers. Total harvest of each age class under the SOFT10 regulations consisted of bulls with S/F or tri-palm or 10 point antlers.

Since the VTRP listed only total point counts, and not counts of points on the brow palms, we assumed all non-S/F bulls harvested in Peace region from 1996 to 2002 during the SOFT period were tri-palms, since only tri-palms were legal. In 2003 during the SOFT10 period, no yearling ($n = 11$) and only one 2-year-old ($n = 4$) bull had ≥ 10 points on one antler; consequently, we assumed the yearlings and other 2-year-old bulls were tri-palms.

Analyses were restricted to potential vulnerability in the Kootenay, Cariboo, and Skeena regions, and to realized vulnerability in the Omineca region due to the consistency of regulations in place throughout the VTRP period (Table 1). As the S/F regulation was implemented part way through the VTRP period in the Okanagan (1993) and Thompson (1993) regions, we were able to determine both potential vulnerability (from any-bull seasons from 1988 to 1992) and realized vulnerability (from S/F seasons combined with LEH bull seasons from 1993 to 2003). Potential vulnerability in the Peace region was determined using VTRP records for August to October GOS harvests from 1988 to 1995 along with GOS harvest records for August only from 1996 to 2003. Realized vulnerability for the Peace region was determined using VTRP records from September through October in each year from 1996 to 2003 when SOFT and SOFT10 regulations were in effect.

We combined samples across years to calculate overall or pooled estimates of potential vulnerability and realized vulnerability of each age class to each of the S/F regulation and the spike-only regulation for each region and the entire province. We also combined samples across years to calculate

potential vulnerabilities to both regulations for each age class of *A. a. andersoni* and *A. a. shirasi* within the Kootenay region using the geographic ranges of each as described by Stent (2010). Similarly, we combined samples across years to calculate potential vulnerabilities for moose in the north-western portion of the Skeena region, assuming Wildlife Management Zone (WMZ) 6f Atlin (BC Ministry of Forests, Lands and Natural Resource Operations 2015) matched the geographic range for *A. a. gigas* as described by Eastman and Ritcey (1987). We calculated 95% confidence intervals for each estimate of vulnerability based on the normal approximation to the binomial distribution (Zar 1984).

We used a 2×2 chi-square contingency table with Yates continuity correction to test for significant differences in potential vulnerabilities of both age classes to both the S/F and spike-only regulations between moose of different subspecies in two areas of British Columbia. First, using pooled samples we compared moose in the Kootenay region within the ranges of *A. a. andersoni* and *A. a. shirasi*. Second, using pooled samples we compared moose in the Skeena region within the ranges of *A. a. gigas* (WMZ 6f Atlin) with moose (*A. a. andersoni*) from adjacent ranges (WMZ 6e Stikine).

We combined samples across years to compare potential vulnerabilities of *A. a. andersoni* among 3 broad geographical zones across British Columbia: the southern zone included the Kootenay, Okanagan, and Thompson regions, the central zone included the Cariboo region, and the northern zone included the Skeena and Peace regions. A 3×2 chi-squared contingency table was used to test for differences between areas for each combination of age class and regulation. Similarly, for each combination of age class and regulation, we used a 6×2

chi-square contingency table to test for differences between regional estimates of potential vulnerability from the pooled sample for the Thompson, Kootenay, Cariboo, Skeena, Peace, and Okanagan regions. Similarly, from the pooled sample for each of the Okanagan, Thompson, Omineca, and Peace regions, we used a 4×2 chi-square contingency table to test for differences between regional estimates of realized vulnerability for each combination of age class and regulation. We used a 2×2 chi-square contingency table with Yates continuity correction to test for differences between potential vulnerability and realized vulnerability of each age class from the pooled sample within the Okanagan, Thompson, and Peace regions.

We determined annual vulnerability, either potential or realized, by region in a

given year for each age class of bull for those years where there were ≥ 25 bulls of that age class with antler point information in the VTRP sample (Table 3). Consequently, we only calculated potential vulnerability of yearlings for 39 of 70 combinations of year and region, and realized vulnerability of yearlings for 33 of 42 combinations of year and region. Similarly, for 2-year-old bulls we calculated potential vulnerability for 47 of 70 combinations of year and region, and realized vulnerability for 20 of 42 combinations of year and region. Central tendency and dispersion of annual vulnerabilities for each combination of regulation/age/region were described by median vulnerability and range of vulnerabilities, respectively. For each estimate of annual vulnerability, we calculated 95% confidence intervals based on the normal

Table 3. Sample sizes for (a) yearling and (b) 2-year-old bull moose from the Voluntary Tooth Return Program (VTRP) for each region/year used in the analyses, British Columbia.

| Year | (a) Yearling bull moose | | | | | | | | (b) 2-year-old bull moose | | | | | | | |
|-------|-------------------------|-----|-----|-------|-------|-------|-----|--------|---------------------------|-----|-----|-------|-------|-------|-----|-------|
| | KO ¹ | OK | TH | CA | OM | SK | PE | Total | KO | OK | TH | CA | OM | SK | PE | Total |
| 1988 | 3 | 2 | 27 | 30 | 202 | 56 | 63 | 383 | 8 | 3 | 43 | 61 | 162 | 99 | 69 | 445 |
| 1989 | 3 | 3 | 26 | 18 | 199 | 96 | 94 | 439 | 16 | 4 | 24 | 51 | 138 | 113 | 74 | 420 |
| 1990 | 11 | 0 | 34 | 20 | 181 | 87 | 62 | 395 | 14 | 3 | 31 | 51 | 119 | 106 | 44 | 368 |
| 1991 | 9 | 0 | 51 | 10 | 158 | 103 | 14 | 345 | 14 | 5 | 58 | 27 | 137 | 95 | 36 | 372 |
| 1992 | 14 | 12 | 81 | 267 | 214 | 80 | 16 | 684 | 34 | 9 | 53 | 136 | 151 | 71 | 27 | 481 |
| 1993 | 14 | 14 | 39 | 225 | 216 | 82 | 14 | 604 | 19 | 5 | 19 | 151 | 189 | 61 | 29 | 473 |
| 1994 | 18 | 9 | 46 | 278 | 250 | 98 | 28 | 727 | 19 | 8 | 16 | 182 | 215 | 77 | 57 | 574 |
| 1995 | 15 | 7 | 31 | 261 | 310 | 217 | 62 | 903 | 25 | 3 | 15 | 164 | 219 | 132 | 68 | 627 |
| 1996 | 24 | 16 | 50 | 251 | 370 | 209 | 18 | 938 | 17 | 5 | 24 | 181 | 247 | 163 | 27 | 664 |
| 1997 | 17 | 16 | 49 | 377 | 357 | 231 | 62 | 1,109 | 31 | 5 | 22 | 231 | 276 | 157 | 22 | 744 |
| 1999 | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a |
| 2000 | 11 | 39 | 65 | 281 | 308 | 253 | 11 | 968 | 18 | 14 | 36 | 139 | 190 | 159 | 3 | 559 |
| 2001 | 9 | 72 | 115 | 352 | 396 | 330 | 38 | 1,312 | 12 | 16 | 34 | 174 | 216 | 185 | 16 | 649 |
| 2002 | 11 | 64 | 98 | 316 | 435 | 356 | 24 | 1,304 | 8 | 16 | 24 | 230 | 223 | 180 | 8 | 689 |
| 2003 | 16 | 87 | 99 | 369 | 418 | 343 | 30 | 1,362 | 26 | 26 | 34 | 251 | 252 | 209 | 12 | 810 |
| Total | 195 | 376 | 887 | 3,434 | 4,460 | 2,781 | 610 | 12,743 | 293 | 126 | 471 | 2,266 | 3,028 | 1,999 | 529 | 8,712 |

¹Region names are abbreviated: KO = Kootenay, OK = Okanagan, TH = Thompson, CA = Cariboo, OM = Omineca, SK = Skeena, and PE = Peace.

approximation to the binomial distribution (Zar 1984).

We used the Kruskal-Wallis single factor analysis of variance to test for differences in annual potential vulnerability of each age class among the Kootenay (only for 2-year-olds), Thompson, Cariboo, Skeena, and Peace regions. Similarly, we used the Kruskal-Wallis single factor analysis of variance to test for differences in annual realized vulnerability of yearlings among the Okanagan, Thompson, Omineca, and Peace regions. We used the Mann-Whitney test to identify differences in annual realized vulnerabilities for 2-year-olds between the Thompson and Omineca regions; the Okanagan and Peace regions were omitted due to small sample size, hence, vulnerability could not be determined for the Peace region and only in a single year for the Okanagan region. Stata 12 was used for all analyses with significance set at $\alpha = 0.05$; statistical testing procedures followed Zar (1984).

Regional trends in annual vulnerability of yearlings to each regulation were illustrated in the Cariboo (potential vulnerability, 1992–2003), Skeena (potential vulnerability, 1988–2003), Thompson (realized vulnerability, 1993–2003) and Omineca (realized vulnerability, 1988–2003). These regions were chosen as there were ≥ 10 years of consistent regulations with $n \geq 25$ yearlings in the VTRP each year. Similarly, regional trends in annual vulnerability of 2-year-old bulls were assessed in the Cariboo, Skeena, and Omineca regions; the Thompson region was omitted as only 4 of 10 years had an adequate sample size. Long-term trends in annual vulnerabilities were illustrated by fitting a third degree polynomial to the data points. The polynomial was employed as it was more sensitive to change than either a linear or log-linear line (Kuzyk 2016, Arsenault et al. 2019).

RESULTS

Teeth and antler point counts were received through the VTRP program for 39,325 bulls from 1 to 23 years of age. Of those, 12,743 (32.4%) were yearling bulls (Table 3a) of which 45% had S/F antlers ($n = 5,779$) with 1,004 spike-only. Antler point counts and teeth were received from a total of 8,712 bulls 2-years old (Table 3b) of which $\sim 9\%$ had S/F antlers ($n = 776$) with 111 spike-only. Only 2.9% of the remaining 17,825 samples (3 to 23 years old) were S/F. Therefore, we used only yearlings and 2-year-old bulls to determine vulnerability. The majority of the VTRP samples came from 3 regions (Cariboo, Skeena, and Omineca) for both yearling (80%) and 2-year-old bulls (84%).

Provincial Vulnerability to the S/F Regulation and Spike-only Regulation

Across British Columbia, potential vulnerability of yearlings to the S/F regulation was 42.7% ($n = 7,123$; 95% CI = 41.6–43.9%) and realized vulnerability was 48.6% ($n = 5,620$; 95% CI = 47.3–50.0%). Potential vulnerability of 2-year-old bulls was 10% ($n = 5,274$; 95% CI = 9.2–10.9%) and realized vulnerability was 7.2% ($n = 3,439$; 95% CI = 6.3–8.0%).

Vulnerability to the spike-only regulation was lower for both age classes across British Columbia. Potential vulnerability of yearlings was 7.8% (95% CI = 7.2–8.4%) and realized vulnerability was 8.7% (95% CI = 7.9–9.4%). Potential vulnerability of 2-year-olds was 1.3% (95% CI = 0.9–1.6%) and realized vulnerability was 1.3% (95% CI = 0.9–1.7%).

Regional Vulnerability to the S/F Regulation

Based on the pooled sample, the potential vulnerability of yearlings to the S/F regulation ranged from 39.2% ($n = 2,781$; 95% CI =

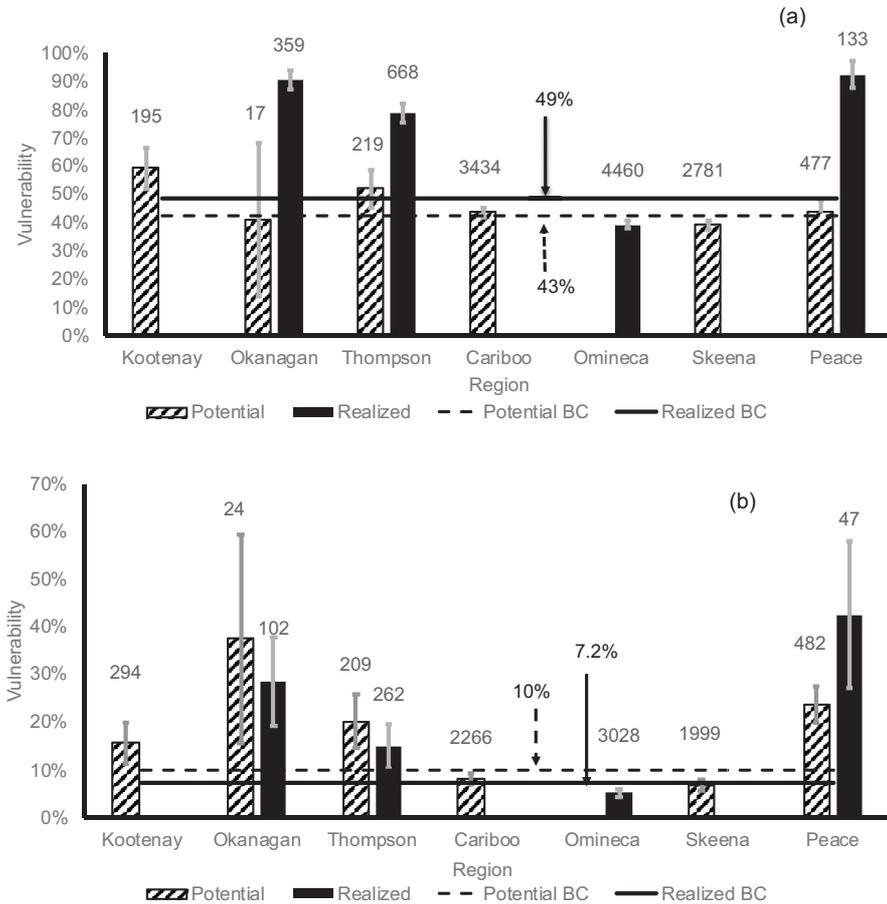


Fig. 3. Vulnerability to the S/F regulation from pooled estimates of (a) yearling bull moose and (b) 2-year-old bull moose in British Columbia. Vertical bars show 95% CI.

37.4–41.1%) in the Skeena region to 59.5% ($n = 195$; 95% CI = 52.3–66.7%) in the Kootenay region (Fig. 3a). Potential vulnerability of yearlings was different among the Thompson, Kootenay, Cariboo, Skeena, Peace, and Okanagan regions ($\chi^2 = 678.4$, $df = 5$, $P < 0.001$). The realized vulnerability of yearlings ranged from 39.5% ($n = 4,460$; 95% CI = 38.0–40.9%) in the Omineca region to 92.5% ($n = 133$; 95% CI = 88.4–97.4%) in the Peace region (Fig. 3a). Realized vulnerability was different ($\chi^2 = 747.2$, $df = 3$, $P < 0.001$) among the Thompson, Omineca, Peace, and Okanagan regions. Realized vulnerability was greater than potential

vulnerability in the Thompson ($\chi^2 = 58.5$, $df = 1$, $P < 0.001$), Peace ($\chi^2 = 99.3$, $df = 1$, $P < 0.001$), and Okanagan regions ($\chi^2 = 38.3$, $df = 1$, $P < 0.001$).

Based on the pooled sample, the potential vulnerability of 2-year-olds to the S/F regulation ranged from 6.8% ($n = 1,999$; 95% CI = 5.7–7.9%) in the Skeena region to 37.5% ($n = 24$; 95% CI = 15.6–59.4%) in the Okanagan region (Fig. 3b). Potential vulnerability was different among the Thompson, Kootenay, Cariboo, Skeena, Peace, and Okanagan regions ($\chi^2 = 185.2$, $df = 5$, $P < 0.001$). The realized vulnerability ranged from 5.2% (95% CI = 4.4–6.0%) in the

Omineca region ($n = 3,028$) to 42.6% ($n = 47$; 95% CI = 27.2–57.9%) in the Peace region (Fig. 3b). Realized vulnerability was also different among the Thompson, Omineca, Peace, and Okanagan regions ($\chi^2 = 198.9$, $df = 3$, $P < 0.001$). Realized vulnerability was greater than potential vulnerability in the Peace region ($\chi^2 = 8.09$, $df = 1$, $P = 0.008$), but not in the Thompson ($\chi^2 = 2.22$, $df = 1$, $P = 0.142$) or Okanagan regions ($\chi^2 = 0.76$, $df = 1$, $P = 0.459$).

Regional Vulnerability to the Spike-Only Regulation

Based on the pooled sample, the potential vulnerability of yearlings to the spike-only regulation ranged from 5.9% ($n = 17$; 95% CI = -0.9–20.4%) in the Okanagan region to 28.2% ($n = 195$; 95% CI = 21.6–34.8%) in the Kootenay region (Fig. 4a). Potential vulnerability was different among the Thompson, Kootenay, Cariboo, Skeena, Peace, and Okanagan regions ($\chi^2 = 152.8$, $df = 5$, $P < 0.001$). The realized vulnerability ranged from 6% ($n = 4,460$; 95% CI = 5.3–6.7%) in the Omineca region to 23.3% ($n = 133$; 95% CI = 15.7–30.9%) in the Peace region (Fig. 4a). Realized vulnerability was different among the Thompson, Omineca, Peace, and Okanagan regions ($\chi^2 = 202.3$, $df = 3$, $P < 0.001$). Realized vulnerability was greater than potential vulnerability in the Peace region ($\chi^2 = 29.8$, $df = 1$, $P < 0.001$) but not in the Thompson ($\chi^2 = 0.0027$, $df = 1$, $P = 0.958$) and Okanagan ($\chi^2 = 1.96$, $df = 1$, $P = 0.215$) regions.

Based on the pooled samples, the potential vulnerability of 2-year-olds to the spike-only regulation ranged from 0% ($n = 24$; 95% CI = -2.1–2.1%) in the Okanagan region to 3.8% ($n = 209$; 95% CI = 1.0–6.7%) in the Thompson region (Fig. 4b). Potential vulnerability was different among the Thompson, Kootenay, Cariboo, Skeena,

Peace, and Okanagan regions ($\chi^2 = 44.8$, $df = 5$, $P < 0.001$). The realized vulnerability ranged from 1.1% in the Omineca region ($n = 3,028$; 95% CI = 0.7–1.5%) to 6.4% in the Peace region ($n = 47$; 95% CI = -1.7–14.5%) (Fig. 4b). Realized vulnerability was different among the Thompson, Omineca, Peace, and Okanagan regions ($\chi^2 = 13.0$, $df = 3$, $P = 0.005$). Realized vulnerability was not greater than potential vulnerability in the Thompson ($\chi^2 = 1.60$, $df = 1$, $P = 0.261$), Peace ($\chi^2 = 0.79$, $df = 1$, $P = 0.420$), and Okanagan regions ($\chi^2 = 0.72$, $df = 1$, $P = 1.000$).

Subspecies Differences in Vulnerability to the S/F Regulation and Spike-only Regulation

Within the Kootenay region, the potential vulnerability of yearling *A. a. shirasisii* bulls was 62.2% ($n = 148$; 95% CI = 54.0–70.3%) and that of *A. a. andersoni* was 50% ($n = 48$; 95% CI = 34.7–65.3%); no difference was found ($\chi^2 = 2.22$, $df = 1$, $P = 0.14$). In contrast, potential vulnerability to the S/F regulation was higher ($\chi^2 = 4.354$, $df = 1$, $P = 0.037$) in 2-year-old *A. a. shirasisii* (18.0%; $n = 228$, 95% CI = 12.8–23.2%) than *A. a. andersoni* bulls (7.5%; $n = 67$, 95% CI = 3.8–14.5%). Similarly, potential vulnerability to the spike-only regulation was higher ($\chi^2 = 5.72$, $df = 1$, $P = 0.017$) in yearling *A. a. shirasisii* (32.4%; $n = 228$, 95% CI = 24.5–40.3%) than *A. a. andersoni* bulls (14.6%; $n = 67$, 95% CI = 3.5–25.7%). Potential vulnerability to the spike-only regulation was similar ($\chi^2 = 0.13$, $df = 1$, $P = 0.72$) in 2-year-old *A. a. shirasisii* (2.2%; $n = 48$, 95% CI = 0.01–4.3%) and *A. a. andersoni* bulls (1.5%; $n = 67$, 95% CI = -0.02–5.2%).

The potential vulnerability of yearlings to the S/F regulation within the purported ranges of *A. a. gigas* (36.2%; $n = 260$, 95% CI = 30.1–42.2%) was not different

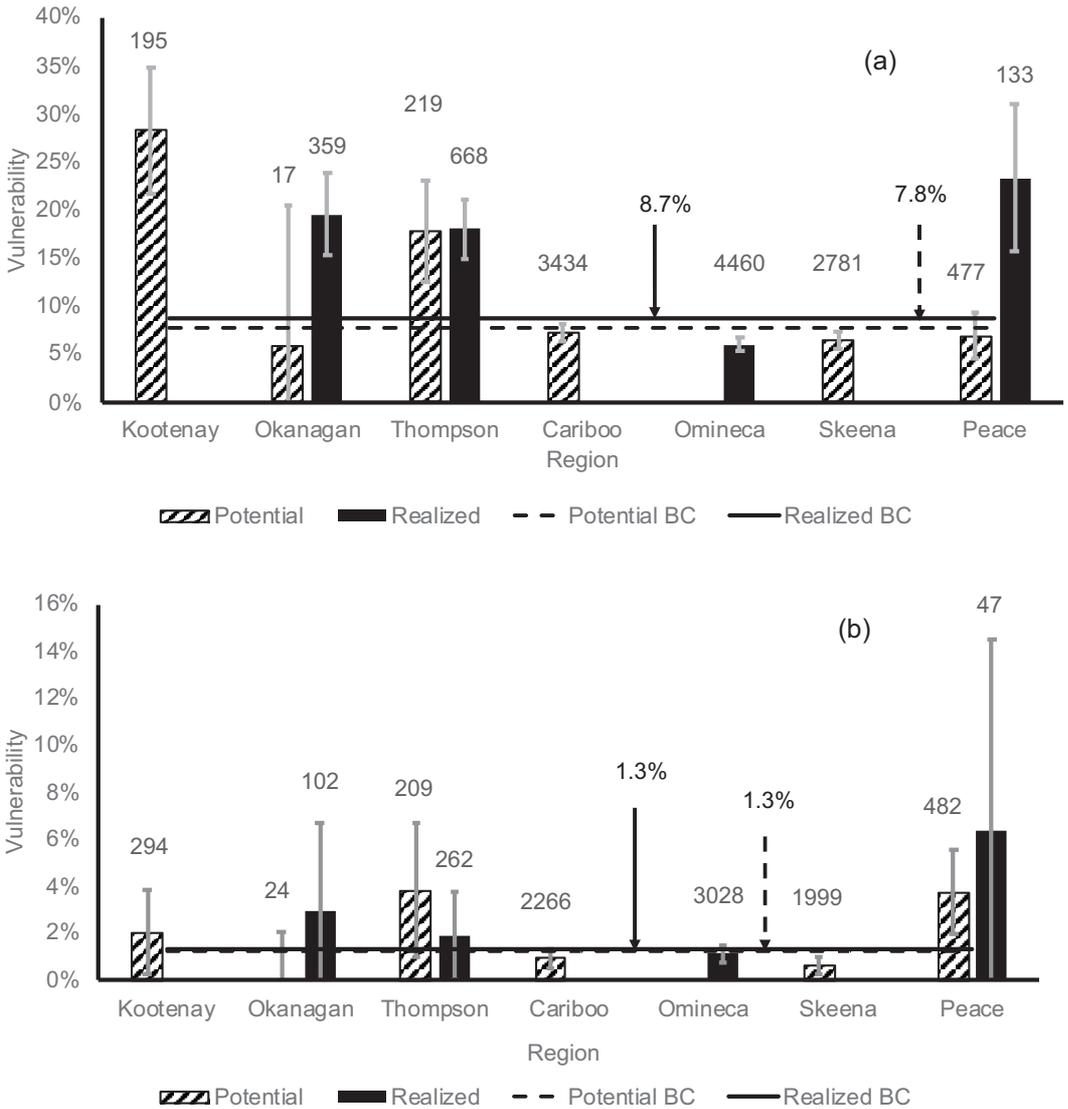


Fig. 4. Vulnerability to the spike-only regulation from pooled estimates for (a) yearling bull moose and (b) 2-year-old bull moose in British Columbia. Vertical bars show 95% CI.

($\chi^2 = 0.039$, $df = 1$, $P = 0.84$) than that of yearlings in adjacent areas with *A. a. andersoni* (35.3%; $n = 260$, 95% CI = 29.2–41.4%). Likewise, there were no differences ($\chi^2 = 0.05$, $df = 1$, $P = 0.82$) between 2-year-old moose within the purported ranges of *A. a. gigas* (4.1%; $n = 269$, 95% CI = 1.5–6.6%) and in adjacent areas with *A. a. andersoni* (4.5%; $n = 245$, 95% CI = 1.7–7.3%).

The potential vulnerability of yearling moose to the spike-only regulation within the purported ranges of *A. a. gigas* (10.8%; $n = 260$, 95% CI = 6.8–14.7%) was similar ($\chi^2 = 0.028$, $df = 1$, $P = 0.87$) to that in adjacent areas with *A. a. andersoni* (10.3%; $n = 252$, 95% CI = 6.4–14.3%). The potential vulnerability of 2-year-old bulls was identical (zero) within the purported ranges of *A.*

a. gigas (0%; $n = 269$, 95% CI = -0.2 – 0.2 %) and in adjacent areas with *A. a. andersoni* (0%; $n = 252$, 95% CI = -0.2 – 0.2 %).

Geographical Differences in Vulnerability to the S/F and spike-only regulations

The potential vulnerability of *A. a. andersoni* yearlings to the S/F regulation was different ($\chi^2 = 17.64$, $df = 2$, $P = 0.0001$) among the southern (Kootenay, Okanagan, Thompson regions) (51.1%; $n = 284$, 95% CI = 45.1 – 57.1 %), central (Cariboo regions) (43.9%; $n = 3,434$, 95% CI = 42.2 – 45.6 %), and northern (Skeena and Peace regions) geographical zones (40.2%; $n = 2,998$, 95% CI = 38.4 – 42.0 %). Potential vulnerability of 2-year-old *A. a. andersoni* bulls was also different ($\chi^2 = 35.94$, $df = 2$, $P < 0.0001$) among the southern (18.7%; $n = 300$, 95% CI = 14.1 – 23.2 %), central (8.1%; $n = 2,266$, 95% CI = 6.9 – 9.2 %), and northern zones (10.8%; $n = 2,212$, 95% CI = 9.5 – 12.1 %).

Similar vulnerability patterns were found for yearling and 2-year-old *A. a. andersoni* bulls to the spike-only regulation. Potential vulnerability of yearling *A. a. andersoni* bulls differed significantly ($\chi^2 = 42.84$, $df = 2$, $P < 0.0001$) among the southern (16.6%; $n = 284$, 95% CI = 12.0 – 21.1 %), central (7.3%; $n = 3,434$, 95% CI = 6.4 – 8.2 %), and northern zones (6.1%; $n = 2,998$, 95% CI = 5.2 – 7.0 %). Potential vulnerability of 2-year-old *A. a. andersoni* bulls was also different ($\chi^2 = 9.54$, $df = 2$, $P = 0.008$) among the southern (3.0%; $n = 300$, 95% CI = 0.9 – 5.1 %), central (0.9%; $n = 2,266$, 95% CI = 0.5 – 1.3 %), and northern zones (1.4%; $n = 2,212$, 95% CI = 0.9 – 1.9 %).

Temporal Differences in Vulnerability to the S/F Regulation

The annual potential vulnerability of yearlings across British Columbia to the S/F

regulation varied from 28 to 90% (median = 43%) (Table 4a). The annual median was ~10% higher in the Thompson region (53%) than in the Peace (40%), Skeena (41%), and Cariboo (44%) regions, but was not different ($H = 4.85$, $df = 3$, $P = 0.18$). The annual vulnerability was highly variable (2–3 x): Peace = 33–71%, Thompson = 42–81%, Skeena = 28–71%, and Cariboo = 35–90%.

The annual realized vulnerability of yearlings across British Columbia to the S/F regulation varied from 26 to 96% (median = 69%) (Table 4a). The annual median was lowest in the Omineca (40%), and ~2x higher in the Thompson (81%), Okanagan (84%), and Peace (93%) regions, and differed among the regions ($H = 25.41$, $df = 3$, $P = 0.001$). The annual realized vulnerability was less variable than the potential vulnerability: Peace = 85–96%, Okanagan = 69–89%, Thompson = 65–86%, and Omineca = 26–51%.

Vulnerability of yearlings to the S/F regulation varied over time in the Cariboo, Skeena, Thompson, and Omineca regions (Fig. 5a and b). In the Cariboo and Skeena regions, potential vulnerability was generally higher (>50%) in the late 1980s and early 1990s than in later years. In contrast, realized vulnerability was generally more consistent in the Omineca region over the entire study period (30–50%), and highest in the Thompson region (70–90%).

The annual potential vulnerability of 2-year-olds across British Columbia to the S/F regulation ranged from 0 to 61% (median = 9%) (Table 4b). The median vulnerability of 2-year-olds was lowest in the Skeena region (5.5%) and highest in the Peace region (26%). No differences were found ($H = 12.743$, $df = 4$, $P = 0.26$) among the Thompson, Kootenay, Cariboo, Skeena, and Peace regions. The largest range of vulnerability was in the Peace region (6.8 to 61.4%) and the smallest in the Skeena region (1.4–16.2%).

Table 4. Medians and ranges of annual % vulnerabilities to the S/F regulation by region for (a) yearling bull moose and (b) 2-year-old bull moose in British Columbia. Vulnerabilities were calculated for each combination of region/year from 1988 to 2003 when there were ≥ 25 moose/year in the VTRP for that combination of region/year.

| Region | (a) Yearling bull moose | | | | (b) 2-year-old bull moose | | | |
|----------|-------------------------|----------------|----------|----------------|---------------------------|----------------|----------|----------------|
| | Potential | | Realized | | Potential | | Realized | |
| | n ¹ | Median (range) | n | Median (range) | n ¹ | Median (range) | n | Median (range) |
| Kootenay | 0 | | n/a | | 5 | 15 (0–19) | n/a | |
| Okanagan | 0 | | 5 | 84 (69–89) | 0 | | 1 | 27 |
| Thompson | 5 | 53 (42–81) | 10 | 81 (65–86) | 4 | 17 (13–45) | 4 | 12 (2.9–15) |
| Cariboo | 12 | 44 (35–90) | n/a | | 15 | 6.6 (2.6–41) | n/a | |
| Omineca | n/a | | 15 | 40 (26–51) | n/a | | 15 | 4.9 (2.1–9.8) |
| Skeena | 15 | 41 (28–71) | n/a | | 15 | 5.5 (1.4–16) | n/a | |
| Peace | 7 | 40 (33–71) | 3 | 93 (85–96) | 8 | 26 (6.8–61) | 0 | |
| Total | 39 | 43 (28–90) | 33 | 69 (26–96) | 47 | 9.1 (0–61) | 20 | 5.5 (2.1–27) |

¹n is the number of years with ≥ 25 moose/year in the VTRP.

The annual realized vulnerability of 2-year-olds across British Columbia to the S/F regulation ranged from 2.1 to 27% (median = 5.5%) (Table 4b). The median vulnerability was $\sim 2.5 \times$ lower in the Omineca region (median 4.9%, range = 2.1–9.8%) than the Thompson region (median 12.2%, range 2.9% to 14.7%), but not different ($H = 2.89$, $df = 1$, $P = 0.09$).

Vulnerability of 2-year-olds to the S/F regulation varied over time in the Cariboo, Skeena, Thompson, and Omineca regions (Fig. 6a and b). Annual potential vulnerability in the Cariboo and Skeena regions was generally higher in the late 1980s and early 1990s ($>10\%$) than later in study period. Annual realized vulnerability in the Omineca region varied between 2 and 10%.

Temporal Differences in Vulnerability to the spike-only Regulation

Annual potential vulnerability for yearlings varied from 1.6 to 37% (median = 7.0%) (Table 5a). Annual potential vulnerability was different among regions ($H = 11.071$, $df = 3$, $P = 0.011$); the Thompson (median = 19.2%)

was higher than the Cariboo (median = 6.8%), Skeena (median = 6.3%), and Peace (median = 8.1%) regions which were similar. The annual range of vulnerability was lowest in the Cariboo region (5.7–10%) and highest in the Thompson region (9.9–37%).

Annual realized vulnerability for yearlings varied from 3.3 to 37% (median = 12%) (Table 5a). The annual range was lowest in the Omineca region (3.3–9.7%) and highest in the Peace region (15–37%). It differed among regions ($H = 23.46$, $df = 3$, $P = 0.0001$) and was lower in the Omineca (median = 6.6%) than in the Thompson (median = 16.6%), Okanagan (median = 18.7%), and Peace regions (median = 27.6%).

Annual potential vulnerability of yearlings varied over time in the Cariboo, Skeena, Thompson, and Omineca regions (Fig. 7a), generally from 5 to 10% in the Cariboo and Skeena regions. Annual realized vulnerability (Fig. 7b) varied from 3 to 10% in the Omineca region and 10 to 25% in the Thompson region.

Annual potential vulnerability of 2-year-olds ranged from 0 to 16.1%, (median = 0.6%)

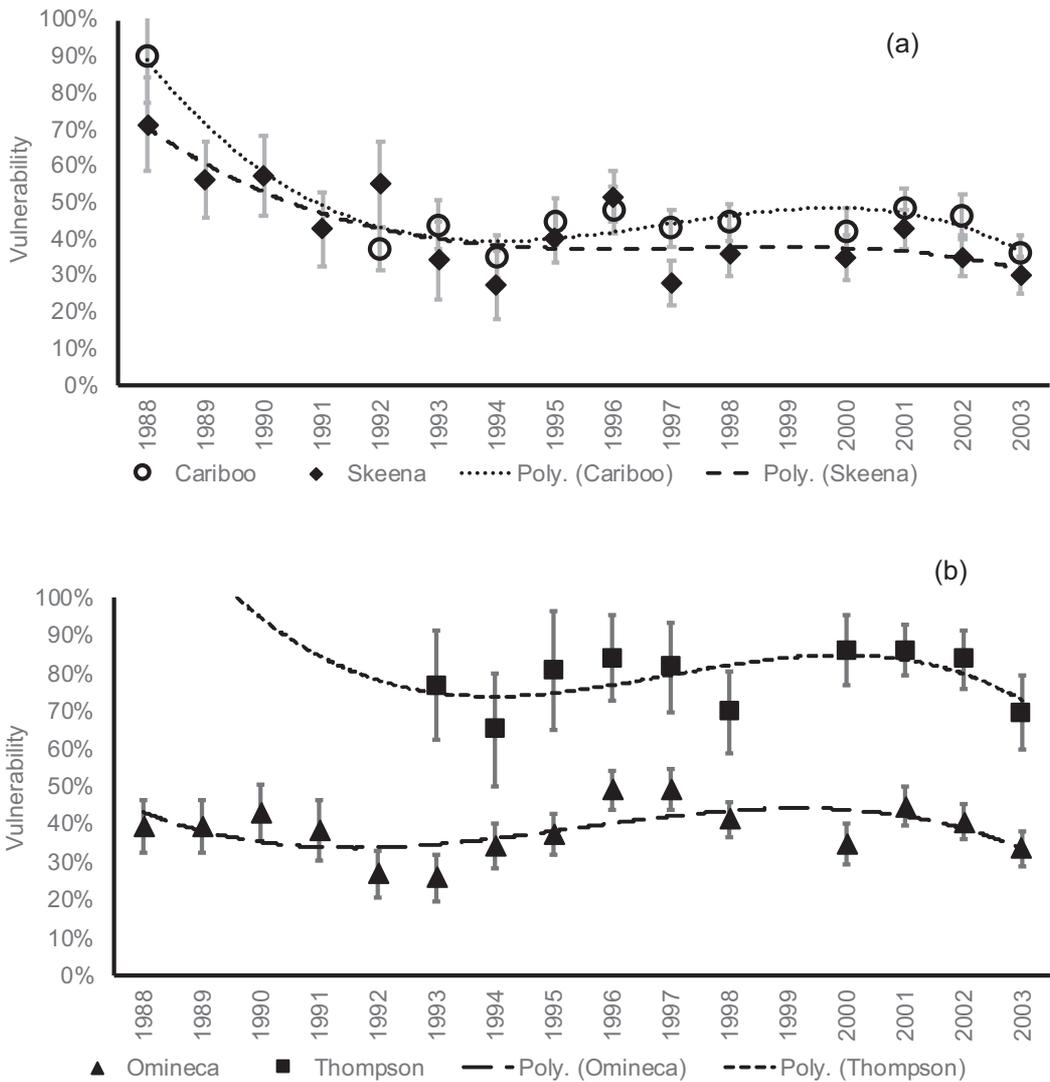


Fig. 5. Regional trends in (a) potential vulnerability of yearlings to the S/F regulation in the Cariboo and Skeena regions, and (b) realized vulnerability of yearlings to the S/F regulation in the Omineca and Thompson regions, British Columbia. Vertical bars show 95% CI. The trends are illustrated by 3rd degree polynomials fit to the data.

(Table 5b). The smallest range of vulnerability was in the Kootenay region region (0%, 5 years) and the largest was in the Thompson region (0–16.1%, 4 years). Although annual potential vulnerability was low overall, it was different among the regions ($H = 16.062$, $df = 4$, $P = 0.0029$), highest in the Thompson (median = 2.7%) and Peace regions (median =

2.8%), and similar in the Kootenay (median = 0%), Cariboo (median = 0.7%), and Skeena regions (median = 0.6%).

Annual realized vulnerability of 2-year-olds ranged from 0 to 5.6% (median = 1.3%) (Table 5b). Annual realized vulnerability was not different among regions ($H = 2.403$, $df = 1$, $P = 0.12$). Annual vulnerability of

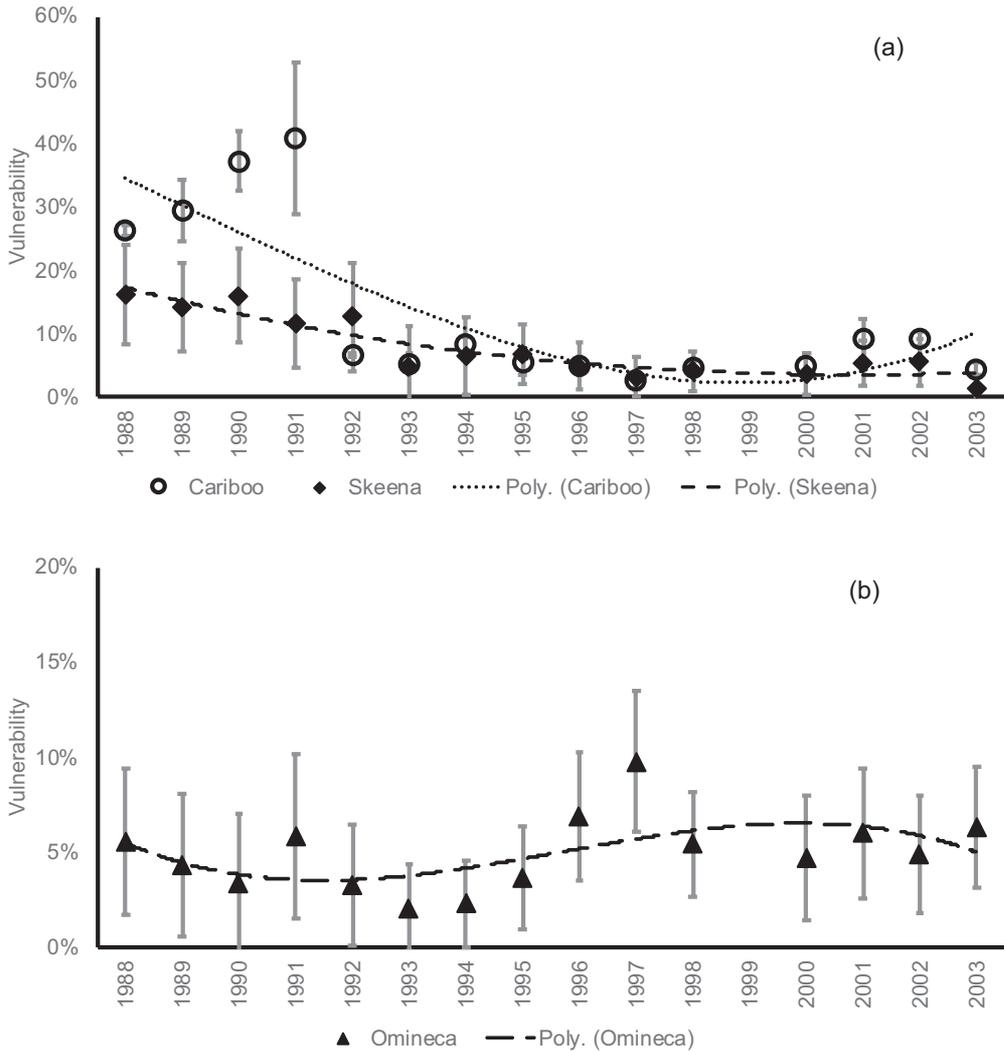


Fig. 6. Regional trends in (a) potential vulnerability of 2-year-olds to the S/F regulation for the Cariboo and Skeena regions, and (b) realized vulnerability of 2-year-olds to the S/F regulation for the Omineca region, British Columbia. Vertical bars show 95% CI. The trends are illustrated by 3rd degree polynomials fit to the data.

2-year-olds varied over time in the Cariboo, Skeena, and Omineca regions (Fig. 8a and b). The potential (Cariboo and Skeena) and realized vulnerabilities (Omineca) were generally <2% each year.

DISCUSSION

We found that ~43% of yearling bull moose in British Columbia were potentially

vulnerable to the S/F regulation, whereas only ~8% were vulnerable to the spike-only regulation. As expected, the potential vulnerability of 2-year-old bulls across the province was lower for both regulations, 10% and 1%, respectively. Our yearling vulnerabilities were similar to those calculated for yearlings in 1980–1991 (some overlap with this study) from VTRP antler point

Table 5. Medians and ranges of annual % vulnerabilities to the spike-only regulation by region for (a) yearling bull moose and (b) 2-year-old bull moose in British Columbia. Vulnerabilities were calculated for each region/year from 1988 to 2003 when there were ≥ 25 moose/year in the VTRP for that combination of region/year.

| Region | (a) Yearling bull moose | | | | (b) 2-year-old bull moose | | | |
|----------|-------------------------|----------------|----------|----------------|---------------------------|----------------|----------|----------------|
| | Potential | | Realized | | Potential | | Realized | |
| | n ¹ | Median (range) | n | Median (range) | n ¹ | Median (range) | n | Median (range) |
| Kootenay | 0 | | n/a | | 5 | 0 (0–0) | n/a | |
| Okanagan | 0 | | 5 | 19 (7.7–24) | 0 | | 1 | 3.8 |
| Thompson | 5 | 19 (9.9–37) | 10 | 17 (12–24) | 4 | 2.7 (0–16) | 4 | 2.8 (0–5.6) |
| Cariboo | 12 | 6.8 (5.7–10) | n/a | | 15 | 0.7 (0–7.4) | n/a | |
| Omineca | n/a | | 15 | 6.6 (3.3–9.7) | n/a | | 15 | 1.1 (0–2.8) |
| Skeena | 15 | 6.3 (3.8–18) | n/a | | 15 | 0.6 (0–2.1) | n/a | |
| Peace | 7 | 8.1 (1.6–18) | 3 | 28 (15–37) | 8 | 2.8 (0–11) | 0 | |
| Total | 39 | 7.0 (1.6–37) | 33 | 12 (3.3–37) | 47 | 0.6 (0–16) | 20 | 1.3 (0–5.6) |

¹n is the number of years with ≥ 25 moose/year in the VTRP.

count data for the S/F (52%) and spike-only (10%) regulations (Hatter 1993). Higher vulnerabilities for yearling bulls likely reflect their smaller antler size (Gasaway et al. 1987, Stewart et al. 2000, Bowyer et al. 2002, Jensen et al. 2013, Androzzi et al. 2015) and lower point counts (Child et al. 2010a) compared to 2-year-olds.

Potential vulnerabilities for both yearling and 2-year-old bulls differed within the ranges of *A. a. shirasi* and *A. a. andersoni* in the Kootenay region, and among southern, central, and northern geographical zones within the range of *A. a. andersoni*. These differences in both age classes across British Columbia presumably reflects the differential antler size for the subspecies (Gasaway et al. 1987), and/or differences in habitat quality (Geist 1987) along the latitudinal breadth of British Columbia.

Based on pooled samples, yearling moose in the Kootenay region had the highest potential vulnerability to both regulations (59% S/F and 28% spike-only). Higher vulnerability to both regulations was observed in areas with *A. a. shirasi* (62% S/F and 32% spike-only) than in areas with *A. a.*

andersoni (50% S/F and 15% spike-only). Similarly, Hatter (1993) found higher vulnerability to the S/F (82%) and spike-only (54%) regulations in yearlings in the eastern portion of the Kootenay region where *A. a. shirasi* were during the 1980–1991 period. In adjacent areas to the west with *A. a. andersoni*, Hatter (1993) found lower vulnerability of yearlings to the S/F (50.8%) and spike-only (9.4%) regulations. We found vulnerability to both regulations was higher for 2-year-old *A. a. shirasi* (18% S/F and 2.2% spike-only) than 2-year-old *A. a. andersoni* (7.5% S/F and 1.5% spike-only). Stent (2010) found higher incidence of S/F antlers in yearling *A. a. shirasi* (69%) than yearling *A. a. andersoni* (48%) in the Kootenay region. Similarly, in bulls 2 years and older, the incidence of S/F antlers, although low overall, was higher in *A. a. shirasi* (6.5%) than *A. a. andersoni* (2.4%). Combined, these studies indicate that vulnerability to the S/F regulation was higher for both age classes of *A. a. shirasi* than *A. a. andersoni*, and consequently, vulnerability in the Kootenay region was higher than in regions without *A. a. shirasi*.

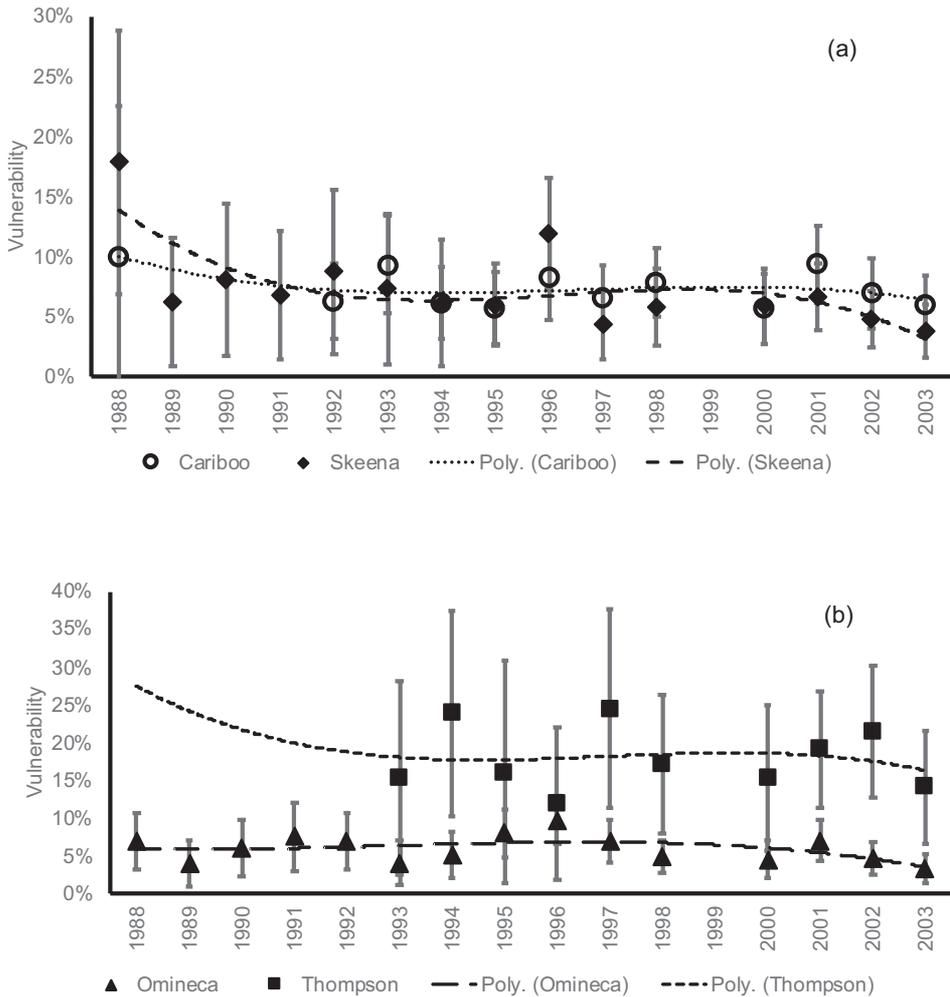


Fig. 7. Regional trends in (a) potential vulnerability of yearlings to the spike-only regulation for the Cariboo and Skeena regions, and (b) realized vulnerability of yearlings to the spike-only regulation for the Omineca and Thompson regions, British Columbia. Vertical bars show 95% CI. The trends are illustrated by 3rd degree polynomials fit to the data.

In the purported range of *A. a. gigas* in the extreme north-western portion of British Columbia (Skeena), potential vulnerability to the S/F regulation was 36% for yearlings and 4.1% for 2-year-olds (VTRP samples). In adjacent areas with *A. a. andersoni*, we found similar potential vulnerability to the S/F regulation for yearlings (35%, $n = 252$) and 2-year-olds (4.5%, $n = 245$). Schwartz et al. (1992) reported that $\sim 50\%$ of *A. a. gigas*

yearling bulls on the Kenai Peninsula (Alaska), but nearly no 2-year-old bulls, were vulnerable to the S/F regulation. Although the vulnerabilities of yearlings in north-western British Columbia were lower than those in Alaska, the vulnerabilities of 2-year-old bulls were intermediate of values in Alaska and British Columbia. Unfortunately, we cannot determine whether moose from the extreme north-western

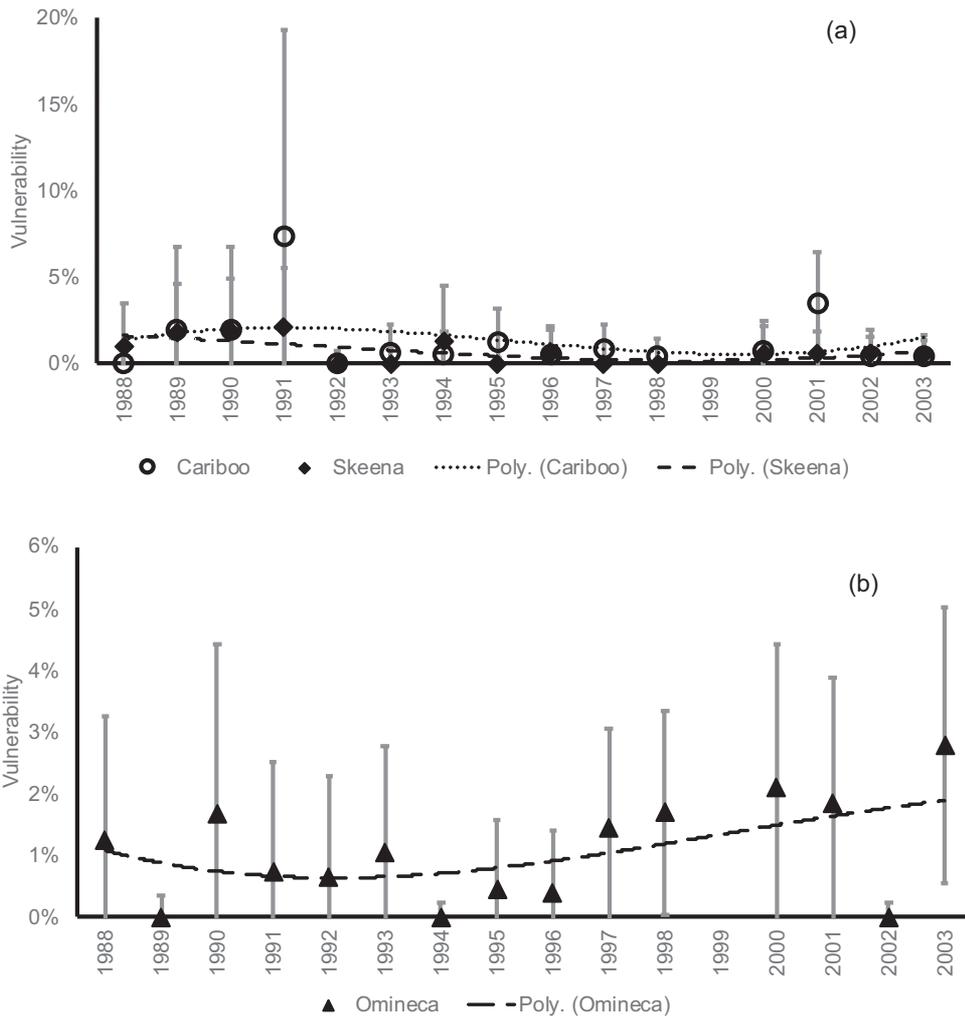


Fig. 8. Regional trends in (a) potential vulnerability of 2-year-olds to the spike-only regulation for the Cariboo and Skeena regions, and (b) realized vulnerability of 2-year-olds to the spike-only regulation for the Omineca region, British Columbia. Vertical bars show 95% CI. The trends are illustrated by 3rd degree polynomials fit to the data.

portion of British Columbia were *A. a. gigas* (Eastman and Ritcey 1987) or *A. a. andersoni* (Hundtermark et al. 2006, Colson 2013, DeCesare et al. 2020).

We found that potential vulnerabilities of yearling and 2-year-olds to the S/F and spike-only regulations were significantly different among regions within the range of *A. a. andersoni*. In general, potential vulnerabilities were generally higher in the southern (Thompson, Okanagan, and

Kootenay) than the central (Cariboo) and northern regions (Peace and Skeena). These differences may reflect the general size increase of moose from south to north (Geist 1987). The vulnerabilities reported by Hatter (1993) for yearlings from the VTRP in 1980–1991 also varied among regions across the range of *A. a. andersoni*, although a distinct, south-to-north pattern was not evident. Our study differed from the work of Hatter (1993) in timing and lengths of

hunting season, sample sizes, and geographic boundaries.

The realized vulnerabilities of both yearling and 2-year-old bulls to the S/F and spike-only regulations were also different among regions within the range of *A. a. andersoni*. Beyond differences in antler structure, the realized vulnerabilities could reflect the variation in availability and harvest rate of >S/F bulls among regions. The realized vulnerability in the Omineca region was much lower than in the Thompson and Okanagan regions, and harvest strategies differed. These 3 regions combined the S/F season with LEH GOS for bulls >S/F, but the S/F season was longer in the Omineca region (BC Ministry of Water, Land and Air Protection 2003–2004), and a larger number of LEH permits were offered there than in the Thompson and Okanagan regions (BC Ministry of Water, Land and Air Protection 2004–2005). Larger numbers of LEH permits in the Omineca likely lead to larger harvests of bulls with >S/F antlers, and lower realized vulnerabilities. Although the timing and length of the hunting seasons were nearly identical in the Omineca and Peace regions, realized vulnerabilities were higher in the Peace region than the Omineca. Because harvest opportunities for non S/F bulls in the Peace region under SOFT or SOFT10 regulations were very restrictive (only bull moose with tri-palm or 10-point antlers were available), lower harvest of bulls with >S/F antlers increased realized vulnerabilities in the Peace region.

The annual estimates of vulnerability within regions in the range of *A. a. andersoni* indicated that the potential and realized vulnerabilities of yearlings to both the spike-fork and spike-only regulations were higher in the late 1980s and late 1990s than in the early 1990s and early 2000s; patterns for 2-year-old bulls were less distinct. This

temporal pattern in antler morphology may reflect the influence of browse quantity and quality related to moose density (Boertje et al. 2007), climate/weather conditions (Murray et al. 2006), and forest practices, including the conversion of moose seasonal ranges to pine and spruce plantations (Rea et al. 2017). For example, herbicide applications (Connor 1992) and mechanical brush cutting (Rea and Gillingham 2001) impose nutritional effects (negative and positive) by affecting browse quality and quantity that influence antler development of yearling and 2-year-old bulls (Young and Boertje 2018). We are currently exploring relationships among moose density, weather/climate, and antler architectures of yearling and 2-year-old moose throughout British Columbia to better understand regional differences in vulnerabilities.

Implementation of the S/F regulation did not result in overharvest of young bulls in the Omineca region. Hatter and Child (1992) found that teen bulls (mostly yearlings and some 2-year-olds) comprised $\geq 30\%$ of the observed bull population in the Omineca region after the hunting season (GOS for S/F combined with LEH for other bulls) in 6 of 9 years from 1982 to 1990. Likewise, bull:cow ratios increased significantly following implementation of the Selective Harvesting System (SHS) on the Kenai Peninsula, Alaska (Schwartz et al. 1992).

Adoption of the S/F regulation in combination with LEH (Thompson and Okanagan regions) or as part of SOFT10 regulations (Peace region) caused regional changes in harvest. By combining moose harvest data (BC Data Catalogue 2021) with age and antler point data from the VTRP, we determined that the average annual bull harvest declined in the Thompson (-50%) and Peace (-72%) regions, but remained relatively unchanged ($+4\%$) in the Okanagan region following adoption of the S/F regulation. The yearling

proportion of the harvest increased in each region (Okanagan 15–53%, Thompson 30–47%, Peace 21–55%) as the proportion of 2-year-old bulls decreased (Okanagan 21–10%, Thompson 28–18%, Peace 17–6.6%). Interestingly, in each region the average annual harvest of yearlings with S/F antlers increased, while conversely, harvest of yearlings with >S/F antlers and 2-year olds with \geq S/F antlers declined.

Further, these shifts in harvest resulted in significantly higher realized than potential vulnerability for yearlings in the 3 regions. Higher realized than potential vulnerabilities in 2-year-olds also occurred in the Peace region, but not in the Okanagan or Thompson regions. Similar changes occurred following adoption of the S/F regulation on the Kenai Peninsula, Alaska where the yearling proportion in the harvest increased from 40% pre-SHS to 64% during the SHS; at the same time, 2–3 year-old bulls declined in the harvest from 38 to 17% (Schwartz et al. 1992). In general, we expected realized vulnerabilities to increase following adoption of the S/F regulation since effort was focused on harvesting bulls with S/F antlers, while the opportunity to harvest larger antlered bulls was reduced by LEH or SOFT regulations. Small sample sizes for 2-year-old bulls during the SOFT period in the Peace region and for yearling and 2-year-old bulls in the Okanagan region prior to adoption of the S/F regulation precluded analysis and interpretation of regional data.

Implementation of the S/F regulation in the Kootenay region in 2009 did not result in overharvest of young bulls. Despite the high potential vulnerability of yearlings (61%) to the S/F regulation, post-hunt surveys during the first 2 years of the GOS for S/F bulls showed that S/F bulls accounted for 3–5% of all moose observed, which was similar to S/F proportions pre-GOS (Szkorupa 2013). Furthermore, there was a similar proportion

of mature bulls in the harvest pre- and post-GOS (Szkorupa 2013). In contrast, recent surveys in the Thompson (BC Ministry of Forests, Lands and Natural Resource Operations and Rural Development 2018, 2019) and Okanagan (Gyug 2013) regions suggest that the harvest of S/F bulls during the GOS, combined with the LEH bull harvest and an unknown male-biased harvest from unlicensed hunting, reduced bull:cow ratios below population objectives in certain areas. Changes to S/F season dates and duration combined with managing hunter access are currently used to better control harvest of yearlings in these regions (C. Procter, pers. comm.).

Hunting regulations and access restrictions are the two management levers most readily available to moose managers throughout British Columbia (BC MFLNRO 2015). Further adjustments to hunting season dates, access restrictions, and antler point restrictions may be required to minimize the risk of overharvesting yearling and 2-year-old bulls. However, further access restrictions and reductions in season length could concentrate hunters in time and space, and possibly increase harvest of S/F bulls on open hunting areas. If further restrictions are required, consideration should be given to shifting from S/F to a spike-only regulation since realized vulnerabilities of yearlings to the spike-only regulation are much lower than to the S/F, and 2-year-olds are essentially not vulnerable to a spike-only regulation. The spike-only regulation offers an alternative for controlling bull harvests while continuing to provide moderate levels of hunting opportunity, and has been used since 2013 to reduce harvest of bulls in several areas of Alaska (Robertia 2013, Alaska Department of Fish and Game 2020–2021).

Our analyses were limited to age and antler point data collected through the VTRP (voluntary) of which the quantity and quality

of submissions may have influenced certain results. In addition, lack of accuracy in tooth aging (Rolandsen et al. 2007) can influence the calculation of vulnerabilities. However, we believe ages determined by our technicians were accurate since this study dealt with yearlings and 2-year-olds, age classes for which determination of age is highly accurate (Rolandsen et al. 2007, Boertje et al. 2015).

The number of submissions to the VTRP varied regionally, but adequate samples were collected from the Kootenay, Thompson, Cariboo, Omineca, and Skeena regions throughout the study where submissions for all bulls ranged from 43.5% (Thompson region) to 57.0% (Kootenay region) of the estimated total harvest of bulls in each region (BC Ministry of Forests, Lands, and Natural Resources Operations, unpublished hunter survey). In contrast, sample size was much lower in the Okanagan region prior to adoption of the S/F regulation – the low submission rate (23.3%) from the small harvest produced inadequate sample sizes ($n = 17$ yearlings and 24 2-year-olds). We also considered VTRP records from the Peace region to be inadequate given the reporting rate was only 11.0% of the estimated bull harvest during the study period. Interestingly, the rates of submission markedly increased in both the Thompson (29.7 to 57.4%) and Okanagan (23.3 to 66.2%) regions following adoption of the S/F regulation, whereas the rate of submissions for the Peace region changed little (12.4 to 9.0%) following adoption of the SOFT regulation.

We assessed the quality of submissions by comparing the similarity of vulnerabilities determined in the Omineca region from the VTRP (Hatter 1993, this study) with studies based on antler inspections by provincial biologists (Hatter and Child 1992, Child et al. 2010b). We found realized vulnerabilities of yearlings in the Omineca

region to the S/F and spike-only regulations were 39.5% and 6.0%, respectively, while vulnerabilities of 2-year-olds were 5.2% and 1.1%, respectively. Hatter (1993) reported 43.5% vulnerability to the S/F regulation and 7% vulnerability to the spike-only regulation for yearlings ($n = 1,490$) from 1980 to 1991. In the Omineca region (1982–1988), Hatter and Child (1992) examined antlers submitted by hunters and found realized vulnerability of yearlings ($n = 166$) was 22.9% to the S/F regulation and 5.4% to the spike-only regulation; realized vulnerability of 2-year-old bulls ($n = 150$) was 2.0% to the S/F regulation and 0.3% to the spike-only regulation.

Child et al. (2010b) examined 1,686 sets of antlers from moose harvested in 1982–1989 and found that the vulnerability of yearling bulls to the S/F regulation was 46%, and the vulnerability of 2-year-old bulls was 8%. The lower vulnerabilities reported by Hatter and Child (1992) may reflect their smaller sample sizes. It was speculated that S/F yearlings were underreported in the earlier studies but no corrections were made, whereas Child et al. (2010b) corrected their sample for underreporting of bulls with S/F antlers. Despite the differences in timing, methods, and sample size, the vulnerabilities calculated from the VTRP by Hatter (1993) and examinations of antlers by Child et al. (2010b) are reasonably similar to those we report here. We believe that the VTRP records indicate that hunters were accurately reporting counts of antler points in the Omineca region, and have no reason to believe otherwise for the other regions.

Non-representative submissions from hunters could be a potential source of bias in the VTRP data and possibly occurred with submissions from the Peace region for yearling and 2-year-old bulls. Potential vulnerability of yearlings region (S/F 43.8%, spike-only 6.9%, $n = 477$) to both

regulations was similar to that in the adjacent in the Skeena region (S/F 39.2%, spike-only 6.4%, $n = 2,781$), but potential vulnerabilities for 2-year-old bulls were higher in the Peace region (S/F 23.7%, spike-only 3.7%, $n = 482$) than in the Skeena region (S/F 6.4%, spike-only 0.7%, $n = 1,999$). The higher potential vulnerability of 2-year-old bulls in the Peace region may reflect submission of a higher than expected number with S/F antlers, or lower than expected number with >S/F antlers compared to the Skeena region.

Realized vulnerability to the S/F regulation in the Peace region for yearlings (92.5%, $n = 133$) and 2-year-olds (42.6%, $n = 47$) was lower than expected, particularly for 2-year-olds. The VTRP records show 7.5% of yearlings ($n = 133$) and 57.4% of 2-year-olds ($n = 47$) had >S/F antlers, which we assume were tri-palm antlers as only bulls with S/F or tri-palm antlers were legal to harvest during the SOFT period. In contrast, inspections of antlers from the Omineca (Child et al. 2010a) indicated <1% of yearlings and 5% of 2-year-olds had tri-palm antlers. Schwartz et al. (1992) reported almost no yearlings or 2-year-olds had tri-palm antlers in Alaska. Thus, lower than expected realized vulnerabilities in the Peace region could reflect submission of lower than expected numbers with S/F antlers, or higher than expected numbers with >S/F antlers.

Although the VTRP had no information on the frequency of tri-palm antlers, it did provide information on number of antler points which allowed us to examine data from the Peace region from another perspective. The VTRP records showed 0.7% of yearlings ($n = 477$) and 1.2% of 2-year-olds ($n = 482$) in the Peace region had antlers with ≥ 10 points during periods when any bull GOS regulations were employed. By comparison, in the adjacent Skeena region

(any bull GOS or LEH), the VTRP records showed 0.04% of yearlings ($n = 2,781$) and 1.25% of 2-year-olds ($n = 1,999$) had antlers with ≥ 10 points. Similarly, in the adjacent Omineca region (LEH and S/F GOS), 0.07% of yearlings ($n = 4,460$) and 0.40% of 2-year-olds ($n = 3,028$) had antlers with ≥ 10 points. This examination suggests similarities in the frequency of antlers with ≥ 10 points among these adjacent regions during GOS or LEH seasons, and supports the observations of Child et al. (2010a) that antlers with ≥ 10 points are rare in yearling and 2-year-old bulls.

In the Omineca region, Child et al. (2010a) reported that 46% of yearling bulls had S/F antlers with <1% having tri-palm or 10-point antlers; 8% of 2-year-old bulls had S/F antlers, and 5% had tri-palm antlers with <1% with 10-point antlers. Applying these antler architectures (Child et al. 2010a) to the Peace region during the periods when SOFT regulations were in use would produce realized vulnerability near 100% for yearlings and $\sim 60\%$ for 2-year-olds. Likewise, few yearling or 2-year-old bulls in Alaska have tri-palm antlers (Schwartz et al. 1992), and applying Alaskan data to the Peace region produced realized vulnerability of nearly 100% for both yearling and 2-year-old bulls.

Both examples produced higher estimates of realized vulnerability for both yearling and 2-year-old bulls than those calculated in the Peace region. We suggest that the unexpected vulnerability of bulls in the Peace region is most likely due to the submission of a number of non-representative samples rather than different antler architectures in the region. Interestingly, the higher than expected potential vulnerability for 2-year-old bulls could arise from an excessive number of 2-year-old bulls with S/F antlers and/or an insufficient number with >S/F antlers in the VTRP. In contrast, the lower

than expected value for realized vulnerability for both yearling and 2-year-old bulls could arise from the opposite scenario. Unfortunately, the low rates of submission limited our analyses of data from the Peace region, particularly during the periods of SOFT (1996–2002) and SOFT10 regulations (2003).

We believe that the vulnerability of bull moose to the S/F and spike-only regulations likely lies somewhere between the potential and realized vulnerabilities we documented. The potential vulnerabilities we report may be low if hunters could not identify spike or fork antlers, if hunters selected against S/F antlered bulls, or if hunters did not report S/F bulls. Bulls with small spike or fork antlers may be under-sampled if they are more difficult to recognize as a bull compared to bulls with larger antler architectures. In addition, hunters may choose to harvest larger antlered bulls in the belief that such a choice would provide more meat or a trophy; lower reporting rates for spike or S/F moose were suspected in earlier studies (Hatter and Child 1992, Hatter 1993, Child et al. 2010b). Hunter selection and/or under reporting could result in under-sampling of S/F bulls in both age classes, thereby lowering their potential vulnerability.

The realized vulnerability estimates we report are high, in some cases approaching 100%. These high values reflect focussed efforts to harvest S/F bulls during a S/F GOS, combined with restricted harvest of larger antlered bulls. If S/F bulls are under reported as described above, even the values we report here may be low. The variation of realized vulnerability among the Okanagan, Thompson, Omineca, and Peace regions may be partly due to different timing and length of S/F GOS between and within the regions. Also, part of the variation may be due to different numbers of permits and different lengths and timing of the

LEH seasons between and within these regions (BC Hunting and Trapping Regulations Synopses and LEH Regulations Synopses accessible at 100.gov.bc.ca). Realized vulnerability will be higher when more S/F bulls or fewer bulls with >S/F antlers are harvested.

Larger numbers of S/F bulls may be harvested if longer S/F seasons are offered, or if seasons coincide with periods of increased vulnerability of S/F bulls. Conversely, offering smaller numbers of LEH tags, or timing LEH seasons to match periods of reduced vulnerability of >S/F bulls may result in fewer large antlered bulls in the harvest. Obviously, if only S/F bulls were available for harvest, the realized vulnerability would be 100%. In the Thompson, Omineca, and Okanagan regions, the harvest of bulls with ≥ 3 points was restricted to varying degrees by offering different numbers of LEH tags. In the Peace region, the SOFT and SOFT10 regulations restricted the harvest of non S/F bulls to those with ≥ 3 points on the brow palm of either antler or those with ≥ 10 points on either antler. As described above, applying the antler architectures for the Omineca region (Child et al. 2010a, 2010b) to the Peace region would produce realized vulnerabilities to the S/F regulation approaching 100% for both yearlings and 2-year-old bulls. More accurate estimates of potential and realized vulnerabilities of yearling and 2-year-old bulls to the S/F regulation can be obtained by requiring mandatory reporting and/or compulsory inspection of all harvested animals.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Based on our analysis of harvest data and others (Hatter and Child 1992, Hatter 1993, Child et al. 2010b), we contend that the S/F regulation applied across British Columbia provided adequate protection of yearlings

and nearly complete protection of 2-year-old bulls under most conditions by focusing harvest on small antlered yearlings and 2-year-olds. We have also shown that the spike-only regulation would have been more conservative than the S/F regulation by focusing harvest on an even smaller proportion of the yearling age class, while providing nearly complete protection for 2-year-old bulls.

In the years since our study period (1988–2003), extensive landscape changes have occurred across British Columbia (Kuzyk and Heard 2014). A mountain pine beetle (*Dendroctonus ponderosae*) outbreak followed by salvage logging has resulted in extensive road construction and large harvested areas throughout the interior of British Columbia (Ritchie 2008), especially in the Omineca, Cariboo, and Skeena regions. Forested areas outside the salvage logging zone have also realized increased access resulting from continued resource development, predominantly industrial forest harvesting. An outbreak of spruce bark beetle (*Dendroctonus rufipennis*) since 2014 (Province of British Columbia 2020) has resulted in further salvage logging operations, mostly in the Omineca region. These ongoing landscape changes have likely raised the vulnerability of moose to harvest by increasing hunter access and reducing security cover (Kuzyk and Heard 2014, Rea et al. 2017). The combination of these impacts that occurred largely after our study period, and the geographical and temporal differences illustrated in this study, point to the continued need for monitoring bull harvests where the S/F regulation is utilized.

Young and Boertje (2018) stressed the importance of understanding the relationship between antler architecture and age, particularly in young bulls in which nutritional stress may retard antler development and subsequently influence sex and

age classifications. Understanding these relationships is particularly important when harvests are regulated by antler architectures. We encourage further investigation of the relationships between antler growth and nutritional status of yearling bulls (e.g., Adams and Pekins 1995) given the changes to, and relationships among, landscape, climate, and range/forage nutrition in British Columbia that influence growth and antler architecture.

Managers considering adopting the S/F regulation or any other antler point-based regulation, should collect and analyse antler architecture and age data to identify those animals vulnerable to antler point-based regulations. Following adoption, data collection should continue to monitor trends in vulnerability and that the regulations target the desired age classes. Furthermore, we recommend that managers quantify the proportion of yearling bulls when conducting population inventory and monitoring. This proportion is always important when monitoring population dynamics (Adams and Pekins 1995, Hatter 2011, Boertje et al. 2019), but especially so under the S/F regulation that effectively focuses harvest on yearlings, yet may impact recruitment into older age classes. Population-level inventories and antler architecture measurements are critically important data that help guide effective conservation and sustainable management of moose populations.

ACKNOWLEDGEMENTS

We would like to thank the thousands of hunters for their voluntary submissions of teeth and antler point-count data which made this study possible. We also thank the following personnel from the BC Ministry of Forests, Lands, Natural Resources Operations and Rural Development: K. Schurmann and G. Kuzyk provided the

VTRP data set for moose that formed the basis of our analysis. G. Kuzyk, C. Procter, S. Marshall, and A. Walker provided constructive comments on earlier drafts which greatly improved this manuscript. We also thank P. Pekins (Editor), E. Bergman (Associate Editor), and 2 anonymous reviewers for their reviews and comments which resulted in further improvements to this manuscript.

REFERENCES

- ADAMS, K. P., and P. J. PEKINS. 1995. Growth patterns of New England moose: yearlings as indicators of population status. *Alces* 31: 53–59.
- AITKEN, D. A., and K. N. CHILD. 1991. Relationship between in-utero productivity of moose and population sex ratios: an exploratory analysis. *Alces* 28: 175–187.
- ALASKA DEPARTMENT OF FISH AND GAME. 2020–2021. Identifying a legal moose. Pages 30–31 in *Alaska Hunting Regulations*. www.adfg.alaska.gov/static/regulations/wildlife_regulations/pdfs/mooseid.pdf (accessed April 2021).
- ANDREOZZI, H. A., P. J. PEKINS, and L. E. KANTAR. 2015. Analysis of age, body weight and antler spread of bull moose harvested in Maine, 1980–2009. *Alces* 51: 45–55.
- ARSENAULT, A. A., A. R. RODGERS, and K. WHALEY. 2019. Demographic status of moose populations in the Boreal Plain Ecozone of Canada. *Alces* 55: 43–60.
- BC (British Columbia) DATA CATALOGUE. 2021. Hunter Sample Moose Survey Estimates 1976 to Current. <https://catalogue.data.gov.bc.ca/dataset/c4977872-347b-40a1-80b3-a5b60cd4dda8/resource/ccaeab19-fdd6-4693-ad25-13574e14d0dd/download/hs-moose-survey-estimates-1976-to-current.xlsx> (accessed March 2021).
- BC (British Columbia) MINISTRY OF ENVIRONMENT. 1981–1982. Hunting Regulations Synopsis. www.a100.gov.bc.ca/appsdata/acat/documents/r22560/BCHunt-Reg-1982.pdf (accessed June 2020).
- _____. 1996–1997. Hunting and Trapping Regulations Synopsis. www.a100.gov.bc.ca/appsdata/acat/documents/r22560/BCHunt-Reg-1997.pdf (accessed June 2020).
- _____. 2016–2018. Hunting and Trapping Regulations Synopsis. Tourism Publications, Ministry of Forests, Lands and Natural Resource Operations, Victoria, British Columbia, Canada.
- _____. 2018–2020. Hunting and Trapping Regulations Synopsis. www.a100.gov.bc.ca/appsdata/acat/documents/r22560/BCHunt-2018-20.pdf
- BC (British Columbia) MINISTRY OF FORESTS, LANDS AND NATURAL RESOURCE OPERATIONS. 2015. Provincial Framework for Moose Management in British Columbia. British Columbia Ministry of Forests, Lands, and Natural Resource Operations, Fish and Wildlife Branch, Victoria, British Columbia, Canada.
- BC (British Columbia) MINISTRY OF FORESTS, LANDS AND NATURAL RESOURCE OPERATIONS and RURAL DEVELOPMENT. 2018. Moose Factsheet. www.env.gov.bc.ca/fw/wildlife/management-issues/docs/2018_Moose_Factsheet.pdf (accessed June 2020).
- _____. 2019. Moose Factsheet. www.env.gov.bc.ca/fw/wildlife/management-issues/docs/2019_Moose_Factsheet.pdf (accessed June 2020).
- BC (British Columbia) MINISTRY OF WATER, LAND AND AIR PROTECTION. 2003–2004. Hunting and Trapping Regulations Synopsis. www.a100.gov.bc.ca/appsdata/acat/documents/r22560/BCHunt-Reg-2004.pdf (accessed June 2020).
- _____. 2004–2005. Limited Entry Hunting Regulations Synopsis. www.a100.gov.bc.ca/appsdata/acat/documents/r22560/leh_04_05.pdf (accessed March 2021).

- BOER, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. *Alces Supplement 1*: 1–10.
- BOERTJE, R. D., M. M. ELLIS, and K. A. KELLIE. 2015. Accuracy of moose age determinations from canine and incisor cementum annuli. *Wildlife Society Bulletin 39*: 383–389. doi: 10.1002/wsb.537
- _____, G. G. FRYE, and D. D. YOUNG, Jr. 2019. Lifetime sex-specific moose mortality during an intentional population reduction. *Journal of Wildlife Management 84*: 6–19. doi: 10.1002/jwmg.21782
- _____, K. A. KELLIE, C. T. SEATON, M. A. KEECH, D. D. YOUNG, B. W. DALE, L. G. ADAMS, and A. R. ADERMAN. 2007. Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. *Journal of Wildlife Management 71*: 1494–1506. doi: 10.2193/2006-159
- BOWYER, R. T., K. M. STEWART, B. M. PIERCE, K. J. HUNDERTMARK, and W. C. GASAWAY. 2002. Geographical variation in antler morphology of Alaskan moose: putative effects of habitat and genetics. *Alces 38*: 155–162.
- BUBENIK, A. B. 1971. Social well-being as a special agent of animal sociology. International Conference on the Behavior of Ungulates and its Relation to Management. 2–5 November 1971, University of Calgary, Calgary, Alberta, Canada.
- _____. 1985. Reproductive strategies in Cervidae. Pages 367–373 in P. F. Fennessy and K. R. Drew, editors. *Biology of Deer Production*. Royal Society of New Zealand Bulletin 22.
- _____. 1987. Behaviour of moose (*Alces alces*) of North America. *Swedish Wildlife Research Supplement 1*: 333–366.
- CANADIAN COUNCIL ON ECOLOGICAL AREAS. 2014. Ecozones of Canada. http://www.ccea.org/Downloads/shapefiles/CA_ecozones_1M_v5_final_map%20v20140213.pdf (accessed January 2019).
- CHILD, K. N. 1983. Selective harvest of moose in the Omineca: some preliminary results. *Alces 19*: 162–177.
- _____. 1996. Moose Harvest Management in British Columbia: Regulation Simplification and Strategy Harmonization. Report to the Wildlife Branch, Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.
- _____, and D. AITKEN. 1989. Selective harvest, hunters, and moose in central British Columbia. *Alces 25*: 81–97.
- _____, _____, and R. V. REA. 2010a. Morphometry of moose antlers in central British Columbia. *Alces 46*: 123–134.
- _____, _____, _____, and R. A. DEMARCHI. 2010b. Potential vulnerability of bull moose in central British Columbia to three antler-based hunting regulations. *Alces 46*: 113–121.
- CHURCH, M., and J. M. RYDER. 2010. Physiography of British Columbia. Pages 17–45 in R. G. Pike, T. E. Redding, R. D. Moore, R. D. Winkler, and K. D. Bladon, editors. *Compendium of Forest Hydrology and Geomorphology in British Columbia*. Land Management Handbook 66, Volume 1 of 2. Ministry of Forests and Range, Forest Science Program, Victoria, British Columbia, Canada.
- COLSON, K. 2013. Genetic Population Structure of Moose (*Alces alces*) at Multiple Spatial Scales. M. S. Thesis. University of Fairbanks, Fairbanks, Alaska, USA.
- CONNOR, J. F. 1992. Impacts of the Herbicide Glyphosate on Moose Browse and Moose Use of four Paired Treated-Control Cutovers Near Thunder Bay, Ontario. M.S. Thesis. School of Forestry, Lakehead University, Lakehead, Ontario, Canada.

- DECESARE, N. J., B. V. WECKWORTH, K. L. PILGRIM, A. B. D. WALKER, E. J. BERGMAN, K. E. COLSON, R. CORRIGAN, R. B. HARRIS, M. HEBBLEWHITE, B. R. JESMER, J. R. SMITH, R. B. TETHER, T. P. THOMAS, and M. K. SCHWARTZ. 2020. Phylogeography of moose in western North America. *Journal of Mammalogy* 101: 10–23. doi: 10.1093/jmammal/gyz163
- DEMARCHI, R. A., and C. L. HARTWIG. 2008. Towards an Improved Moose Management Strategy for British Columbia. Habitat Conservation Trust Fund Report CAT07-0-0325. Victoria, British Columbia, Canada.
- EASTMAN, D., and R. RITCEY. 1987. Moose habitat relationships and management in British Columbia. *Swedish Wildlife Research Supplement 1*: 101–117.
- GASAWAY, W. C., D. J. PRESTON, D. J. REED, and D. J. ROBY. 1987. Comparative antler morphology and size of North American Moose. *Swedish Wildlife Research Supplement 1*: 311–325.
- GEIST, V. 1987. On the evolution and adaptations of *Alces*. *Swedish Wildlife Research Supplement 1*: 11–23.
- GYUG, L. W. 2013. Okanagan Moose Inventory 2012–2103. Report for Fish and Wildlife Branch, British Columbia Ministry of Forests, Lands and Natural Resource Operations, Penticton, British Columbia, Canada.
- HATTER, I. W. 1993. Yearling Moose Vulnerability to Spike-Fork Regulation. Memo report. Wildlife Branch, British Columbia Environment, Victoria, British Columbia, Canada.
- _____. 1998. Moose Conservation and Harvest Management in Central and Northern British Columbia. Draft for Stakeholder Discussion. Wildlife Branch, British Columbia Environment, Victoria, British Columbia, Canada.
- _____. 1999. An evaluation of moose harvest management in Central and Northern British Columbia. *Alces* 35: 91–103.
- _____, and K. N. CHILD. 1992. An evaluation of a spike-fork bull moose antler regulation in central British Columbia. Proceedings of the 1991 Moose Harvest Workshop, Kamloops, British Columbia. Wildlife Branch, British Columbia Environment, Victoria, British Columbia, Canada.
- HATTER, J. 2011. Early Ecology and Management of the Moose in Central British Columbia. Reprint of “The Moose of Central British Columbia”, 1950 Ph. D. Thesis, State College of Washington, Pullman, Washington, USA. Island Blue Print/Printorium Bookworks, Victoria, British Columbia, Canada.
- HUNDTMARK, K. J., R. T. BOWYER, G. F. SHIELDS, C. C. SCHWARTZ, and M. H. SMITH. 2006. Colonization history and taxonomy of moose *Alces alces* in southeastern Alaska inferred from mtDNA variation. *Wildlife Biology* 12:331–338. doi: 10.2981/0909-6396(2006)12[331:CHATOM]2.0.CO;2
- JENSEN, W. F., J. R. SMITH, J. J. MASKEY Jr., J. V. MCKENZIE, and R. E. JOHNSON. 2013. Mass, morphology, and growth rates of moose in North Dakota. *Alces* 49: 1–15.
- KUZYK, G. 2016. Provincial population and harvest estimates of moose in British Columbia. *Alces* 52: 1–11.
- _____, and D. HEARD. 2014. Research Design to Determine Factors Affecting Moose Population Change in British Columbia: Testing the Landscape Change Hypothesis. *Wildlife Bulletin* No. B-126. British Columbia Ministry of Forests, Lands, and Natural Resource Operations, Victoria, British Columbia, Canada.
- MACGREGOR, W. G., and K. N. CHILD. 1981. Changes in moose management in British Columbia. *Alces* 17: 64–76.

- MURRAY, D. L., E. W. COX, W. B. BALLARD, H. A. WHITLAW, M. S. LENARZ, T. W. CUSTER, T. BARNETT, and T. K. FULLER. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs* 166: 1–30. doi:10.2193/0084-0173(2006)166[1:PNDACI]2.0.CO;2
- POOLE, K., and C. DEMARS. 2015. Review of Moose Management in the Peace Region of British Columbia. Report prepared for British Columbia Ministry of Forests, Lands and Natural Resource Operations, Fish and Wildlife Section, Fort St. John, British Columbia, Canada.
- PROVINCE OF BRITISH COLUMBIA. 2020. Omineca Spruce Beetle Outbreak. www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/forest-pests/bark-beetles/spruce-beetle/omineac-spruce-beetle (accessed June 2020).
- REA, R. V., K. N. CHILD, and D. A. AITKEN. 2017. Seeing the forests for their hoofage and stumpage values. *British Columbia Forest Professional* 24: 18–19.
- _____, and M. P. GILLINGHAM. 2001. The impact of the timing of brush management on the nutritional value of woody browse for moose *Alces alces*. *Journal of Applied Ecology* 38: 710–719. doi:10.1046/j.1365-2664.2001.00641.x
- RITCHIE, C. 2008. Management and challenges of the Mountain Pine Beetle infestation in British Columbia. *Alces* 44: 127–135.
- ROBERTIA, J. 2013. 10 illegal moose taken on Alaska's Kenai Peninsula as hunters adapt to new rules. *Anchorage Daily News*, 16 September 2013. www.adn.com (accessed April 2021).
- ROLANDSEN, C. M., E. J. SOLBERG, M. HEIM, F. HOLMSTRON, M. I. SOLEM, and B. -E. SAETHER. 2007. Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. *European Journal of Wildlife Research*. doi:10.1007/s10344-007-0100-8
- SCHWARTZ, C. C., K. J. HUNDERTMARK, and T. H. SPRAKER. 1992. An evaluation of selective bull moose harvest on the Kenai Peninsula, Alaska. *Alces* 28: 1–13.
- SERGEANT, D. E., and D. H. PIMLOTT. 1959. Age determination in moose from sectioned incisor teeth. *Journal of Wildlife Management* 23: 315–321. doi:10.2307/3796891
- STENT, P. 2010. Kootenay Moose Composition Surveys: Winter 2009/10. Ministry of Environment, Environmental Stewardship Division, Cranbrook, British Columbia, Canada.
- STEWART, K. M., R. T. BOWYER, J. G. KIE, and W. C. GASAWAY. 2000. Antler size relative to body mass in moose: tradeoffs associated with reproduction. *Alces* 36: 77–83.
- SZKORUPA, T. 2013. Kootenay Moose General Open Season Monitoring. Final Project Report. Habitat Conservation Trust Foundation, Victoria, British Columbia, Canada.
- TIMMERMANN, H. R. 1987. Moose harvest strategies in North America. *Swedish Wildlife Research Supplement* 1: 565–579.
- _____. 1992. Moose sociobiology and implications for harvest. *Alces* 28: 59–77.
- YOUNG, D. D., and R. D. BOERTJE. 2018. Age-related antler characteristics in an intensively managed and nutritionally stressed moose population. *Alces* 54: 37–44.
- ZAR, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.